

GLOBAL DYNAMICS OF SOME SPATIALLY
HETEROGENEOUS POPULATION MODELS

FANG ZHANG



GLOBAL DYNAMICS OF SOME SPATIALLY HETEROGENEOUS POPULATION MODELS

by

©Fang Zhang

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Abstract

The conjoining of nonlinear dynamics and biology has brought about significant advances in both areas, with biology promoting developments in the theory of dynamical systems and nonlinear dynamics providing a tool for understanding biological phenomena. Since the 1970's, various differential equations models have been proposed to study the evolutionary (long term) behavior of interacting species, the transmission of infectious diseases, biological invasions and disease spread. The purpose of this PhD thesis research project is to investigate the global dynamics and traveling waves in some spatially heterogeneous population models.

In chapter 1, we present some elementary concepts and theorems based on the theories of uniform persistence and coexistence state, chain transitive sets, monotone dynamics, spreading speeds and traveling waves.

In chapter 2, we study the global dynamics of a non-autonomous predator-prey system with dispersion. We establish sufficient conditions for uniform persistence and global extinction, the existence, uniqueness, and global stability of the positive periodic solutions. After that, we lift these results to asymptotically periodic systems.

It has been observed that population dispersal affects the spread of many infectious

diseases. An epidemic model in a patchy environment with periodic coefficients is investigated in chapter 3. Motivated by the works of Wang and Zhao [51], we present a disease transmission model with population dispersal among n patches, and we assumed that these coefficients are periodic with a common period due to the seasonal effects. We focus mainly on establishing a threshold between the extinction and the uniform persistence of the disease, and the conditions under which the positive periodic solution is globally asymptotically stable.

In the book [41], L. Rass and J. Radcliffe raised an open problem on the spreading speed and traveling waves for an epidemic model on the integer lattice Z . We address this problem in chapter 4 by appealing to the theory of spreading speeds and traveling waves for monotone semiflows [34]. More precisely, we establish the existence of asymptotic speeds of spread, and show that this spreading speed coincides with the minimal wave speed for monotone traveling waves.

Chapter 5 is devoted to the investigation of the asymptotic behavior for a reaction-diffusion model with a quiescent stage, which was proposed by Haderler and Lewis [18]. By appealing to the theory of spreading speeds and traveling waves for monotone semiflows, we establish the existence of asymptotic speed of spread and show that it coincides with the minimal wave speed for monotone traveling waves. By the theory of monotone dynamical systems and the persistence theory, we prove a threshold type result on the global stability of either the zero solution or a unique positive steady state in the case where the spatial domain is bounded.

To illustrate the obtained mathematical results, we also provide numerical simulations in chapters 2–5.

At last, we summarize the results we have obtained in the thesis, and also point out some problems for future research in chapter 6.

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Chapter 1

Preliminaries

In this chapter, we present some terminologies and known results which will be used in this thesis. They are involved in global attractors, uniform persistence, chain transitive sets, monotone dynamical systems, and the newly developed theory for spreading speeds and traveling waves.

1.1 Uniform persistence and chain-transitive sets

Let (X, d) be a complete metric space with metric d . Recall that the Kuratowski measure of noncompactness, α , is defined by

$$\alpha(B) = \inf\{r : B \text{ has a finite cover of diameter } < r\},$$

for any bounded set B of X .

Definition 1.1.1 *Let X be a metric space with metric d and $f : X \rightarrow X$ a continuous map. A bounded set A is said to attract a bounded set B in X if $\lim_{n \rightarrow \infty} \sup_{x \in B} \{d(f^n(x), A)\} = 0$. A subset $A \subset X$ is said to be an attractor for f if A is nonempty, compact and invariant ($f(A) = A$), and A attracts some open neighborhood U of itself. A global attractor for $f : X \rightarrow X$ is an attractor that attracts every point in X .*

Definition 1.1.2 A continuous mapping $f : X \rightarrow X$ is said to be α -condensing if f takes bounded sets to bounded sets and $\alpha(f(B)) < \alpha(B)$ for any nonempty closed bounded set $B \subset X$ with $\alpha(B) > 0$; asymptotically smooth if for any nonempty closed bounded set $B \subset X$ for which $f(B) \subset B$, there is a compact set $J \subset B$ such that J attracts B .

Theorem 1.1.1 [63, Theorem 1.1.2] If $f : X \rightarrow X$ is asymptotically smooth and point dissipative, and if orbits of bounded sets are bounded, then there exists a connected global attractor A that attracts each bounded set in X .

Definition 1.1.3 Let $f : X \rightarrow X$ be a continuous map and $A \subset X$ be a nonempty invariant set for f . We say A is internally chain-transitive if for any $a, b \in A$ and any $\epsilon > 0$, there is a finite sequence x_1, \dots, x_m in A with $x_1 = a, x_m = b$ such that $d(f(x_i), x_{i+1}) < \epsilon, 1 \leq i \leq m-1$. The sequence $\{x_1, \dots, x_m\}$ is called an ϵ -chain in A connecting a and b .

Let $\omega > 0$ be fixed. We consider a periodic system of ordinary differential equations

$$\begin{cases} \frac{dx}{dt} = F(t, x) \\ x(0) = x_0 \in \mathbb{R}_+^n, \end{cases} \quad (1.1)$$

where $x = (x_1, \dots, x_n) \in \mathbb{R}^n$ and $\mathbb{R}_+^n = \{x \in \mathbb{R}^n : x_i \geq 0, 1 \leq i \leq n\}$. We assume that $F : \mathbb{R}_+^1 \times \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ is continuous and ω -periodic in t , that all partial derivatives $\frac{\partial F_i}{\partial x_j}, 1 \leq i, j \leq n$, exist and are continuous on $\mathbb{R}_+^1 \times \mathbb{R}_+^n$, and that every solution $\phi(t, x)$ of (1.1) satisfying $\phi(0, x) = x \in \mathbb{R}_+^n$ exists globally on $[0, \infty]$.

By the proof of [63, Lemma 5.1.1], it is easy to see the following result holds.

Theorem 1.1.2 *Assume that there exists some $1 \leq i \leq n$, such that $F_i \geq x_i F_{0i}(t, x)$, $\forall (t, x) \in \mathbb{R}_+^1 \times \mathbb{R}_+^n$, where $F_{0i} : \mathbb{R}_+^{n+1} \rightarrow \mathbb{R}_+^n$ is continuous and ω -periodic in t . If*

$$u^*(t) = (u_1^*(t), \dots, u_{i-1}^*(t), 0, u_{i+1}^*(t), \dots, u_n^*(t))$$

is a nonnegative ω -periodic solution of (1.1) such that $\int_0^\omega F_{0i}(t, u^(t)) dt > 0$, then there exists $\delta > 0$ such that*

$$\limsup_{n \rightarrow \infty} d(\phi(n\omega, x), u^*(0)) \geq \delta, \forall x \in \text{Int}(\mathbb{R}_+^n).$$

Let $f : X \rightarrow X$ be a continuous map and $X_0 \subset X$ an open set. Define $\partial X_0 = X \setminus X_0$, and $M_\partial = \{x \in \partial X_0 : f^n(x) \in \partial X_0, \forall n \geq 0\}$, which may be empty.

Definition 1.1.4 *A function $f : X \rightarrow X$ is said to be uniformly persistent with respect to $(X_0, \partial X_0)$ if there exists $\eta > 0$ such that $\liminf_{n \rightarrow \infty} d(f^n(x), \partial X_0) \geq \eta$ for all $x \in X_0$.*

Definition 1.1.5 *Let X be a complete metric space with metric d , and let $\omega > 0$. A family of mappings $T(t) : X \rightarrow X, t \geq 0$, is called an ω -periodic semiflow on X if it possesses the following properties:*

(1) $T(0) = I$, where I is the identity map on X ;

(2) $T(t + \omega) = T(t) \circ T(\omega), \forall t \geq 0$;

(3) $T(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$.

In particular, if (2) holds for any $\omega > 0$, $T(t)$ is called an autonomous semiflow.

Let $T(t) : X \rightarrow X$, $t \geq 0$, be an ω -periodic semiflow with $T(t)X_0 \subset X_0$, $\forall t \geq 0$.

The following three abstract results will be used in our analysis of periodic systems.

Theorem 1.1.3 [63, Theorem 3.1.1] *Let $T(t)$ be an ω -periodic semiflow on X with $T(t)X_0 \subset X_0$, $\forall t \geq 0$. Assume that $S := T(\omega)$ is point dissipative in X and compact. Then the uniform persistence of S with respect to $(X_0, \partial X_0)$ implies that of $T(t) : X \rightarrow X$.*

Theorem 1.1.4 [63, Theorem 1.3.1] *Assume that*

- (1) $f(X_0) \subset X_0$ and f has a global attractor A ;
- (2) *There exists a finite sequence $\mathcal{M} = \{M_1, \dots, M_k\}$ of disjoint, compact and isolated invariant sets in ∂X_0 such that*
 - (a) $\Omega(M_\partial) := \cup_{x \in M_\partial} \omega(x) \subset \cup_{i=1}^k M_i$;
 - (b) *No subset of \mathcal{M} forms a cycle in ∂X_0 ;*
 - (c) M_i is isolated in X ;
 - (d) $W^s(M_i) \cap X_0 = \emptyset$ for each $1 \leq i \leq k$.

Then there exists $\delta > 0$ such that for any compact internally chain-transitive set L with $L \not\subset M_i$ for all $1 \leq i \leq k$, we have $\inf_{x \in L} d(x, \partial X_0) > \delta$. In particular, f is uni-

formly persistent in the sense that there exists $\eta > 0$ such that $\liminf_{n \rightarrow \infty} d(f^n(x), \partial X_0) \geq \eta$ for all $x \in X_0$.

Theorem 1.1.5 [63, Theorem 1.3.6] *Let X be a closed subset of a Banach space $(E, \|\cdot\|)$, X_0 be a convex and relatively open subset in X , and $f : X \rightarrow X$ be a continuous map with $f(X_0) \subset X_0$. Assume that $f : X \rightarrow X$ is point dissipative and compact, and that f is uniformly persistent with respect to $(X_0, \partial X_0)$. Then there exists a global attractor A_0 for $f : X_0 \rightarrow X_0$, and f has a coexistence state $x_0 = f(x_0) \in A_0$.*

Theorem 1.1.6 [37, Theorem 3.7] *Let $f : X \rightarrow X$ be a continuous map with $f(X_0) \subset X_0$. Assume that $f : X \rightarrow X$ is asymptotically smooth and uniformly persistent, and that f has a global attractor A . Then $f : X_0 \rightarrow X_0$ has a global attractor A_0 .*

Theorem 1.1.7 [37, Theorem 4.7] *Let X be a closed and convex subset of a Banach space $(E, \|\cdot\|)$, $X_0 \subset X$ be open and convex in E , and $\Phi(t) : X \rightarrow X$ be a continuous-time semiflow on X with $\Phi(t)(X_0) \subset X_0, \forall t \geq 0$. Assume that $\Phi(t)$ is α -condensing for each $t > 0$, and that $\Phi(t) : X_0 \rightarrow X_0$ has a global attractor A_0 . Then $\Phi(t)$ has an equilibrium $x_0 \in A_0$.*

Let $f : U \times \Lambda \rightarrow U$ be continuous, where $U \subset X$, X is a Banach space, and Λ is a metric space with metric ρ . We write $f_\lambda = f(\cdot, \lambda)$ and use the notation $B_X(x, s)(B_\Lambda(\lambda, s))$ for the open ball of radius s about the point $x \in X$ ($\lambda \in \Lambda$). For a linear operator A on X , we write $r(A)$ for its spectral radius.

Theorem 1.1.8 [44] *Let $(x_0, \lambda_0) \in U \times \Lambda$, $B_X(x_0, \delta) \subset U$ for some $\delta > 0$ and assume that $D_x f(x, \lambda)$ exists and is continuous in $B_X(x_0, \delta) \times \Lambda$. Suppose that $f(x_0, \lambda_0) = x_0$, $r(D_x f(x_0, \lambda_0)) < 1$, and $f_{\lambda_0}^n(x) \rightarrow x_0$ for every $x \in U$. In addition, suppose that*

(1) *For each $\lambda \in \Lambda$, there is a set $B_\lambda \subset U$ such that for each $x \in U$, there exists an integer $N = N(x, \lambda)$ such that $f_\lambda^N(x) \in B_\lambda$;*

(2) *$C = \overline{\bigcup_{\lambda \in \Lambda} f_\lambda(B_\lambda)}$ is compact in U .*

Then there exist $\epsilon_0 > 0$ and a continuous map $\hat{x} : B_\Lambda(\lambda_0, \epsilon_0) \rightarrow U$ such that $\hat{x}(\lambda_0) = x_0$, $f(\hat{x}(\lambda), \lambda) = \hat{x}(\lambda)$, and $f_\lambda^n x \rightarrow \hat{x}(\lambda)$, $\forall x \in U, \lambda \in B_\Lambda(\lambda_0, \epsilon_0)$.

For each $\lambda \in \Lambda$, let $S_\lambda : X \rightarrow X$ be a continuous map such that $S_\lambda(x)$ is continuous in (λ, x) . Assume that every positive orbit for S_λ has compact closure in X , and that the set $\bigcup_{\lambda \in \Lambda, x \in X} \omega_\lambda(x)$ has compact closure, where $\omega_\lambda(x)$ denotes the omega limit of x for discrete semiflow $\{S_\lambda^n\}$.

Theorem 1.1.9 [63, Theorem 1.4.2] *Assume that $S_\lambda(X_0) \subset X_0, \forall \lambda \in \Lambda$. Let $\lambda_0 \in \Lambda$ be fixed, and assume further that*

(1) *$S_{\lambda_0} : X \rightarrow X$ has a global attractor, and there exists an acyclic covering*

$\{M_1, \dots, M_k\}$ of $\Omega(M_\partial)$ for f in ∂X_0 ;

(2) *There exists $\delta_0 > 0$ such that for any $\lambda \in \Lambda$ with $\rho(\lambda, \lambda_0) < \delta_0$ and any $x \in X_0$,*

$$\limsup_{n \rightarrow \infty} d(S_\lambda^n(x), M_i) \geq \delta_0, 1 \leq i \leq k.$$

Then there exists $\delta > 0$ such that $\liminf_{n \rightarrow \infty} d(S_\lambda^n(x), \partial X_0) \geq \delta$ for any $\lambda \in \Lambda$ with $\rho(\lambda, \lambda_0) < \delta$ and for any $x \in X_0$.

To study asymptotically periodic systems, we also need the following three results.

Theorem 1.1.10 [63, Lemma 1.2.2] *Let $T_n : X \rightarrow X$, $n \geq 0$, be an asymptotically autonomous discrete process with limit $S : X \rightarrow X$. Then the omega limit set of any precompact orbit of $\{T_n\}$ is internally chain transitive for S .*

Theorem 1.1.11 [63, Theorem 1.2.1] *Let A be an attractor, and C a compact internally chain transitive set for $S : X \rightarrow X$. If $C \cap W^s(A) \neq \emptyset$, then $C \subset A$.*

Theorem 1.1.12 [63, Theorem 1.2.2] *Assume that each fixed point of f is an isolated invariant set, that there is no cyclic chain of fixed points, and that every precompact orbit converges to some fixed point of f . Then any compact internally chain-transitive set is a fixed point of f .*

1.2 Monotone dynamics

Let (E, P) be an ordered Banach space with the positive cone P having nonempty interior $\text{Int}(P)$. For $x, y \in E$, we write $x \geq y$ if $x - y \in P$, $x > y$ if $x - y \in P \setminus \{0\}$, and $x \gg y$ if $x - y \in \text{Int}(P)$.

Definition 1.2.1 *Let U be a subset of E , and $f : U \rightarrow U$ a continuous map. The map f is said to be monotone if $x \geq y$ implies that $f(x) \geq f(y)$; strictly monotone if $x > y$ implies that $f(x) > f(y)$; strongly monotone if $x > y$ implies that $f(x) \gg f(y)$.*

Theorem 1.2.1 (*Dancer-Hess Lemma*) [11, Proposition 1] *Let $u_1 < u_2$ be fixed points of the strictly monotone continuous mapping $f : U \rightarrow U$, let $I := [u_1, u_2] \subset U$, and assume that $f(I)$ is precompact and f has no fixed point distinct from u_1 and u_2 in I . Then either*

(1) *there exists an entire orbit $\{x_n\}_{n \rightarrow -\infty}^\infty$ of f in I such that $x_{n+1} > x_n, \forall n \in \mathbb{N}$,*

and $\lim_{n \rightarrow -\infty} x_n = u_1$ and $\lim_{n \rightarrow \infty} x_n = u_2$, or

(2) *there exists an entire orbit $\{y_n\}_{n \rightarrow -\infty}^\infty$ of f in I such that $y_{n+1} < y_n, \forall n \in \mathbb{N}$, and*

$\lim_{n \rightarrow -\infty} y_n = u_2$ and $\lim_{n \rightarrow \infty} y_n = u_1$.

Definition 1.2.2 *A continuous map $f : X \rightarrow X$ is said to be subhomogeneous if $f(\lambda x) \geq \lambda f(x)$ for any $x \in X$ and $\lambda \in [0, 1]$; strictly subhomogeneous if $f(\lambda x) > \lambda f(x)$ for any $x \in X$ with $x \gg 0$ and $\lambda \in (0, 1)$.*

Theorem 1.2.2 [62, Lemma 1] *Let either $V = [0, b]_E$ with $b \gg 0$, or $V = P$. Assume $f : V \rightarrow V$ is continuous, strongly monotone and strictly subhomogeneous on V . Then f admits at most one positive fixed point in V .*

Theorem 1.2.3 [63, Theorem 2.3.4] *Let $V = [0, b]_E$ with $b \gg 0$ and $f : V \rightarrow V$ be a continuous map. Assume that*

(1) *$f : V \rightarrow V$ is strongly monotone and strictly subhomogeneous;*

(2) *$f : V \rightarrow V$ is asymptotically smooth, and every positive orbit of f in V is bounded;*

(3) $f(0) = 0$, and the derivative $Df(0)$ is compact and strongly positive.

Let $r(Df(0))$ be the spectral radius of $Df(0)$. Then the following statements are valid:

(a) If $r(Df(0)) \leq 1$, then every positive orbit in V converges to 0;

(b) If $r(Df(0)) > 1$, then there exists a unique fixed point $u^* \gg 0$ in V such that every positive orbit in $V \setminus \{0\}$ converges to u^* .

1.3 Spreading speeds and traveling waves

Let \mathbb{C} be the set of all bounded and continuous functions from \mathbb{H} to \mathbb{R}^k , where $\mathbb{H} = \mathbb{R}$ or \mathbb{Z} . We regard any vector in \mathbb{R}^k as a function in \mathbb{C} .

For $\varsigma = (\varsigma_1, \dots, \varsigma_k), \xi = (\xi_1, \dots, \xi_k) \in \mathbb{C}$, we write $\varsigma \geq \xi$ ($\varsigma \gg \xi$) provided $\varsigma_i(x) \geq \xi_i(x)$ ($\varsigma_i(x) > \xi_i(x)$), $\forall 1 \leq i \leq k, x \in \mathbb{H}$, and $\varsigma > \xi$ provided $\varsigma \geq \xi$ but $\varsigma \neq \xi$. For any two vectors a, b in \mathbb{R}^k , we can define $a \geq (>, \gg) b$ similarly. For any $r \in \mathbb{R}^k$ with $r \gg 0$, we define

$$\mathbb{R}_r^k := \{u \in \mathbb{R}^k : r \geq u \geq 0\}, \quad \mathbb{C}_r := \{u \in \mathbb{C} : r \geq u \geq 0\}$$

We always equip \mathbb{R}^k with the norm $\|(u_1, \dots, u_k)\| = \max\{|u_i| : 1 \leq i \leq k\}$ and the positive cone \mathbb{R}_+^k , so that \mathbb{R}^k is an ordered Banach space. We also equip \mathbb{C} with the compact open topology, that is, $u^n \rightarrow u$ in \mathbb{C} means that the sequence of $u^n(x)$ converges to $u(x)$ as $n \rightarrow \infty$ uniformly for x in any compact subset of \mathbb{H} . Moreover,

we define the metric function $d(\cdot, \cdot)$ in \mathbb{C} with respect to this topology by

$$d(u, v) = \sum_{k=0}^{\infty} \frac{\max_{|x| \leq k} ||u(x) - v(x)||}{2^k}, \quad \forall u, v \in \mathbb{C},$$

so that (\mathbb{C}, d) is a metric space.

Define the reflection operator \mathcal{R} by $\mathcal{R}[u](x) = u(-x)$. Given $h \in \mathbb{H}$, define the translation operator $T_h[u](x) = u(x - h)$. Let $v \gg 0$ in \mathbb{R}^k and $Q : \mathbb{C}_v \rightarrow \mathbb{C}_v$. We impose the following hypotheses on Q :

$$(A1) \quad Q[\mathcal{R}[u]] = \mathcal{R}[Q[u]], \quad T_h[Q[u]] = Q[T_h[u]], \quad \forall h \in \mathbb{H}.$$

$$(A2) \quad Q : \mathbb{C}_v \rightarrow \mathbb{C}_v \text{ is continuous with respect to the compact open topology.}$$

$$(A3) \quad \{Q(u)(x) : u \in \mathbb{C}_v, x \in \mathbb{H}\} \text{ is a precompact subset of } \mathbb{R}^k.$$

$$(A4) \quad Q : \mathbb{C}_v \rightarrow \mathbb{C}_v \text{ is monotone (order preserving) in the sense that } Q[u] \geq Q[\bar{u}] \text{ whenever } u \geq \bar{u}.$$

Note that the hypothesis (A1) implies that $Q[u] \in \mathbb{R}_v^k$ whenever $u \in \mathbb{R}_v^k$. Thus, Q is also a map from \mathbb{R}_v^k to \mathbb{R}_v^k .

$$(A5) \quad Q : \mathbb{R}_v^k \rightarrow \mathbb{R}_v^k \text{ admits exactly two fixed points } 0 \text{ and } v, \text{ and for any } \epsilon > 0, \text{ there is } \alpha \in \mathbb{R}_v^k \text{ with } ||\alpha|| < \epsilon \text{ such that } Q[\alpha] \gg \alpha.$$

By [34, Theorems 2.11 and 2.15], it then follows that the discrete-time semiflow $\{Q^n\}_{n=0}^{\infty}$ (in short, the map Q) on \mathbb{C}_v admits an asymptotic speed of spread c^* . A linear operators approach was also developed in [34] to estimate the spreading speed c^* of Q . Let $M : \mathbb{C} \rightarrow \mathbb{C}$ be a linear operator with the following properties:

- (B1) M is continuous with respect to the compact open topology.
- (B2) M is a positive operator, that is, $M[u] \geq 0$ whenever $u > 0$.
- (B3) For any uniformly bounded subset A of \mathbb{C} , the set $\{M[u](x) : u \in A, x \in \mathbb{H}\}$ is bounded in \mathbb{R}^k .
- (B4) $M[\mathcal{R}[u]] = \mathcal{R}[M[u]]$, $T_h[M[u]] = M[T_h[u]]$, $\forall u \in \mathbb{C}, h \in \mathbb{H}$.
- (B5) M can be extended to a linear operator on the linear space

$$\bar{\mathbb{C}} := \{u = u_1 e^{\mu_1 x} + u_2 e^{\mu_2 x} : u_1, u_2 \in \mathbb{C}, \mu_1, \mu_2 \in \mathbb{R}, x \in \mathbb{H}\},$$

such that if $u_n, u \in \bar{\mathbb{C}}$ and $u_n(x) \rightarrow u(x)$ uniformly on any bounded set, then $M[u_n](x) \rightarrow M[u](x)$ uniformly on any bounded set.

By property (B4), M is also a linear operator on \mathbb{R}^k . Define the linear map $B_\mu : \mathbb{R}^k \rightarrow \mathbb{R}^k$ by

$$B_\mu[\sigma] = M[\sigma e^{-\mu x}](0), \quad \forall \sigma \in \mathbb{R}^k.$$

In particular, $B_0 = M$ on \mathbb{R}^k . If $\sigma_n, \sigma \in \mathbb{R}^k$ and $\sigma_n \rightarrow \sigma$ as $n \rightarrow \infty$, then $\sigma_n e^{-\mu x} \rightarrow \sigma e^{-\mu x}$ uniformly on any bounded subset of \mathbb{H} . Thus, $B_\mu[\sigma_n] = M[\sigma_n e^{-\mu x}](0) \rightarrow M[\sigma e^{-\mu x}](0) = B_\mu[\sigma]$, and hence B_μ is continuous. Moreover, B_μ is a positive operator on \mathbb{R}^k . Assume that

- (B6) For any $\mu \geq 0$, B_μ is a positive operator, and there is n_0 such that $B_\mu^{n_0} = \underbrace{B_\mu B_\mu \dots B_\mu}_{n_0}$ is a compact and strongly positive linear operator on \mathbb{R}^k .

(B7) The principal eigenvalue $\lambda(0)$ of B_0 is larger than 1.

Let $\Phi(\mu) = \frac{1}{\mu} \ln \lambda(\mu)$, $\mu \geq 0$, where $\lambda(\mu)$ is the principal eigenvalue of B_μ . The following result is useful for the estimate of the spreading speed.

Theorem 1.3.1 [34, Theorem 3.10] *Let Q be an operator on \mathbb{C}_v satisfying (A1)-(A5) and c^* be the asymptotic speed of spread of Q . Assume that the linear operator M satisfies (B1)-(B7), and that the infimum of $\Phi(\mu)$ is attained at some finite value μ^* and $\Phi(\infty) > \Phi(\mu^*)$. Then the following statements are valid:*

(1) *If $Q[u] \leq M[u]$ for all $u \in \mathbb{C}_v$, then $c^* \leq \inf_{\mu > 0} \Phi(\mu)$.*

(2) *If there is some $\eta \in \mathbb{R}^k$, with $\eta \gg 0$, such that $Q[u] \geq M[u]$ for any $u \in \mathbb{C}_\eta$, then $c^* \geq \inf_{\mu > 0} \Phi(\mu)$.*

Recall that a family of operators $\{Q_t\}_{t \geq 0}$ is said to be a semiflow on \mathbb{C}_v if it satisfies

(i) $Q_0(u) = u, \forall u \in \mathbb{C}_v$.

(ii) $Q_{t_1}[Q_{t_2}[u]] = Q_{t_1+t_2}[u], \forall t_1, t_2 \geq 0, u \in \mathbb{C}_v$.

(iii) $Q(t, u) := Q_t(u)$ is continuous in (t, u) on $[0, \infty) \times \mathbb{C}_v$.

We have the result on spreading speeds of continuous-time semiflows.

Theorem 1.3.2 [34, Theorem 2.17] *Let $\{Q_t\}_{t \geq 0}$ be a semiflow on \mathbb{C}_v with $Q_t[0] = 0$, $Q_t[v] = v$ for all $t \geq 0$. Suppose that for any $t > 0$, the map Q_t satisfies all hypotheses*

(A1)-(A5), and let c^* be the asymptotic speed of spread of the map Q_1 . Then the following statements are valid:

(1) For any $c > c^*$, if $u \in \mathbb{C}_v$ with $0 \leq u \ll v$, and $u(x) = 0$ for x outside a bounded

interval, then $\lim_{t \rightarrow \infty, |x| \geq tc} Q_t[u](x) = 0$.

(2) For any $c < c^*$ and any $\alpha \in \mathbb{R}_v^k$ with $\alpha \gg 0$, there is a $r_\alpha > 0$ such that if $u \in \mathbb{C}_v$

with $u(x) \geq \alpha$ for x on an interval of length $2r_\alpha$, then $\lim_{t \rightarrow \infty, |x| \leq tc} Q_t[u](x) = v$.

If, in addition, Q_1 is subhomogeneous, then r_α can be chosen to be independent of $\alpha \gg 0$.

We say that $W(x - ct)$ is a traveling wave of the semiflow $\{Q_t\}_{t \geq 0}$ if $W : \mathbb{R} \rightarrow \mathbb{R}^k$ and $Q_t[W](x) = W(x - ct)$, and that $W(x - ct)$ connects v to 0 if $W(-\infty) = v$ and $W(\infty) = 0$.

Given a function $u \in \mathbb{C}_v$ and a bounded interval $I = [a, b] \subset \mathbb{H}$. We define a function $u_I \in C(I, \mathbb{R}^k)$ by $u_I(x) = u(x)$. Moreover, for any subset \mathcal{D} of \mathbb{C}_v , we define $\mathcal{D}_I = \{u_I \in C(I, \mathbb{R}^k) : u \in \mathcal{D}\}$. In order to obtain the existence of the traveling wave with the wave speed $c \geq c^*$, we need the following assumption:

(A6) For any number $\varsigma > 0$, there exists $\iota = \iota(\varsigma) \in [0, 1)$ such that for any $\mathcal{D} \subset \mathbb{C}_v$ and any interval $I = [a, b]$ of the length ς , we have $\alpha(Q[\mathcal{D}]_I) \leq \iota \alpha(\mathcal{D}_I)$, where α is the Kuratowski measure of noncompactness on the Banach space $C(I, \mathbb{R}^k)$.

We remark that if \mathbb{H} is discrete, then the hypothesis (A3) on Q implies the hypothesis (A6). The subsequent result implies that the spreading speed of $\{Q_t\}_{t \geq 0}$,

described in Theorem 1.3.2, is also the minimal wave speed for monotone traveling waves.

Theorem 1.3.3 [34, Theorems 4.3 and 4.4]/[33, Remark 2.3] *Let $\{Q_t\}_{t \geq 0}$ be a semi-flow on \mathbb{C}_v with $Q_t[0] = 0$, $Q_t[v] = v$ for all $t \geq 0$. Assume that for any $t > 0$, the map Q_t satisfies all hypotheses (A1)-(A5), and let c^* be the asymptotic speed of spread of the map Q_1 . Then the following statements are valid:*

- (1) *For any $0 < c < c^*$, $\{Q_t\}_{t \geq 0}$ has no traveling wave $W(x - ct)$ connecting v to 0.*
- (2) *Furthermore, if Q_t satisfies (A6), then for any $c \geq c^*$, $\{Q_t\}_{t \geq 0}$ has a traveling wave $W(x - ct)$ connecting v to 0 such that $W(s)$ is continuous and non-increasing in $s \in \mathbb{R}$.*

Chapter 2

A Nonautonomous Predator-Prey Model

In this chapter, we study the global dynamics of a nonautonomous predator-prey system with dispersion. By appealing to the theory of nonautonomous semiflows, we establish sufficient conditions for uniform persistence and global extinction. The global stability of the positive periodic solutions is also obtained via the Liapunov function method.

This chapter is organized as follows. In Section 2.1, we present the model and the research background. Section 2.2 is devoted to establishing uniform persistence and global stability of positive periodic solution. In Section 2.3, we obtain sufficient conditions for global extinction of the predator species, and provide numerical simulations. These results are lifted to asymptotically periodic systems in Section 2.4.

2.1 Introduction

One of the fundamental problems in population dynamics is to study the evolutionary (long-term) behavior of the interacting species. In order to take into account the dispersal phenomenon of species, Levin [30] presented an autonomous Lotka-Volterra type model in a patchy environment. Kishimoto [29] and Takeuchi [46] also studied

this kind of model, but all the coefficients in their systems are constants. For more autonomous models in patchy environments, we refer to [2], [10], [19] and references therein. However, it is much more realistic to assume that all the intraspecific coefficients and dispersive coefficients depend on time. In addition, it is natural to assume that these coefficients are periodic with a common period due to the seasonal effects. In 1998, Song and Chen [45] analyzed the following model,

$$\begin{cases} \frac{dx_1}{dt} = x_1(a_1(t) - b_1(t)x_1 - c(t)y) + D_1(t)(x_2 - x_1) \\ \frac{dx_2}{dt} = x_2(a_2(t) - b_2(t)x_2) + D_2(t)(x_1 - x_2) \\ \frac{dy}{dt} = y(-d(t) + e(t)x_1 - q(t)y). \end{cases} \quad (2.1)$$

Here x_1 and y , respectively, are population densities of prey species x and predator species y in patch 1, and x_2 is the density of prey species x in patch 2. Predator species y is confined to patch 1, while the prey species x can disperse between two patches. $D_i(t)$ ($i = 1, 2$) are dispersal coefficients of prey species x . Under the assumption that $a_i(t)$, $b_i(t)$, $D_i(t)$ ($i = 1, 2$), $c(t)$, $d(t)$, $e(t)$, $q(t)$ are all continuous, ω -periodic and strictly positive functions, Song and Chen [12] obtained sufficient conditions for the uniform persistence and the global attractivity of positive periodic solution for system (2.1). We should point out that those conditions in [45] are in terms of the maximum and minimum values of the periodic coefficient functions. It is more desirable to establish natural conditions in terms of average integrals of certain functions over the interval $[0, \omega]$. More recently, Cui, Takeuchi and Lin [9] studied a different class of predator-prey systems with dispersion. See, e.g., [6], [17], [25], [60], [61] for other

types of nonautonomous models in patchy environments.

In this chapter, we will study a general periodic predator-prey system with dispersion,

$$\begin{cases} \frac{dx_1}{dt} = x_1 g_1(x_1, y, t) + D_1(t)(x_2 - x_1) \\ \frac{dx_2}{dt} = x_2 g_2(x_2, t) + D_2(t)(x_1 - x_2) \\ \frac{dy}{dt} = y g_3(x_1, y, t). \end{cases} \quad (2.2)$$

Motivated by the biological interpretations of model (2.1), we assume that

$$(H1) \quad \frac{\partial g_1(x_1, y, t)}{\partial x_1} < 0, \quad \frac{\partial g_1(x_1, y, t)}{\partial y} < 0, \quad \frac{\partial g_2(x_2, t)}{\partial x_2} < 0, \quad \frac{\partial g_3(x_1, y, t)}{\partial x_1} > 0, \quad \frac{\partial g_3(x_1, y, t)}{\partial y} < 0, \\ g_3(0, 0, t) < 0.$$

(H2) There is $M_1 > 0$ such that $g_1(M_1, 0, t) \leq 0, g_2(M_1, t) \leq 0, \forall t \geq 0$; and for each

$B > 0$, there is $N_1 = N_1(B) > 0$ such that $g_3(B, N_1, t) \leq 0, \forall t \geq 0$.

Biologically, the first two inequalities in (H1) imply that the per-capita growth rate of the prey population in patch 1 decreases both with the prey density in the same patch and with the predator density. The first one is due to a limited resource or crowding effect, and the second one is a consequence of predation. Similarly, the third and fifth inequalities hold because of a limited resource, and the fourth inequality implies that the per-capita growth rate of the predator population in patch 1 increases with the prey density in the same patch, which is a consequence of predation. The last inequality in (H1) implies that the population density of the predator decreases if only very small amount of predator and no prey are living in patch 1. The first

condition in (H2) implies that the prey population starts to decrease when there are plenty of them living in one patch, even without absence of the predator. This is due to the carrying capacity for the prey population. The second condition in (H2) means that with the limited amount of prey population, the predator population starts to decrease when there are plenty of them living in one patch.

It is observed that sometimes the coefficient functions in model (2.1) are not periodic, but are asymptotic to periodic functions. We also consider the asymptotically periodic system

$$\begin{cases} \frac{dx_1}{dt} = x_1 \bar{g}_1(x_1, y, t) + \bar{D}_1(t)(x_2 - x_1) \\ \frac{dx_2}{dt} = x_2 \bar{g}_2(x_2, t) + \bar{D}_2(t)(x_1 - x_2) \\ \frac{dy}{dt} = y \bar{g}_3(x_1, y, t) \end{cases} \quad (2.3)$$

under the following two assumptions:

(H3) $\lim_{t \rightarrow \infty} (\bar{D}_i(t) - D_i(t)) = 0$, and $\lim_{t \rightarrow \infty} (\bar{g}_i(x_1, x_2, y, t) - g_i(x_1, x_2, y, t)) = 0$ uniformly for (x_1, x_2, y) in bounded subsets of \mathbb{R}_+^3 .

(H4) There is M_2 such that $\bar{g}_1(x_1, 0, t) \leq 0, \bar{g}_2(x_2, t) \leq 0, \forall x_1, x_2 \geq M_2, t \geq 0$; and for each $B > 0$, there is $N_2 = N_2(B) > 0$ such that $\bar{g}_3(B, y, t) \leq 0, \forall y \geq N_2, t \geq 0$.

2.2 Persistence and positive periodic solutions

In this section, we study the uniform persistence, existence and global stability of positive periodic solution of periodic system (2.2).

For the two-dimensional subsystem

$$\begin{cases} \frac{dx_1}{dt} = x_1 g_1(x_1, 0, t) + D_1(t)(x_2 - x_1) \\ \frac{dx_2}{dt} = x_2 g_2(x_2, t) + D_2(t)(x_1 - x_2), \end{cases} \quad (2.4)$$

we have the following result.

Lemma 2.2.1 *Let ρ be the principal Floquet multiplier of the linear system resulting from the linearization of (2.4) at $x(t) \equiv 0$. Then the following statements are valid:*

- (1) *If $\rho > 1$, then (2.4) admits a unique positive ω -periodic solution $(x_1^*(t), x_2^*(t))$, and it is globally asymptotically stable for (2.4) in $\mathbb{R}_+^2 \setminus \{0\}$;*
- (2) *If $\rho \leq 1$, then $(0, 0)$ is a globally asymptotically stable periodic solution of (2.4) in \mathbb{R}_+^2 .*

In particular, there holds $\rho > 1$ provided that

$$(M1) \text{ either } m(g_1(0, 0, t)) := \frac{1}{\omega} \int_0^\omega g_1(0, 0, t) dt > m(D_1(t)), \text{ or } m(g_2(0, t)) > m(D_2(t)).$$

Proof. For simplicity, we write system (2.4) as

$$\frac{dx}{dt} = F^1(t, x), \quad (2.5)$$

$$\text{with } x = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}, F^1(t, x) = \begin{pmatrix} x_1 g_1(x_1, 0, t) + D_1(t)(x_2 - x_1) \\ x_2 g_2(x_2, t) + D_2(t)(x_1 - x_2) \end{pmatrix}.$$

Obviously, $(0, 0)$ is a ω -periodic solution of (2.5). The corresponding linear periodic system of (2.5) is

$$\frac{dz}{dt} = D_x F^1(t, 0)z. \quad (2.6)$$

Let I be the 2×2 identity matrix and let $\phi(t)$ be the fundamental matrix solution of (2.6) with $\phi(0) = I$. By the continuity and differentiability of solutions with respect to initial values, it easily follows that the Poincaré map S associated with (2.5) is defined in a neighborhood of $(0, 0)$, and the derivative $DS(0) = \phi(\omega)$. Thus, $\rho = r(\phi(\omega)) = r(DS(0))$. Moreover, by assumption (H2), there exists $M_1 > 0$ such that $g_1(M_1, 0, t) \leq 0, g_2(M_1, t) \leq 0, \forall t \geq 0$. It then follows that for any $M \geq M_1$, the set $[0, M]^2$ is positively invariant set for system (2.4). By Theorem 1.2.3 with the order interval $V = [0, M]^2, \forall M \geq M_1$, it follows that the conclusions (1) and (2) hold. Note that

$$\begin{aligned} D_x F^1(t, 0) &= \begin{pmatrix} g_1(0, 0, t) - D_1(t) & D_1(t) \\ D_2(t) & g_2(0, t) - D_2(t) \end{pmatrix} \\ &\geq \begin{pmatrix} g_1(0, 0, t) - D_1(t) & 0 \\ 0 & g_2(0, t) - D_2(t) \end{pmatrix} := B(t). \end{aligned}$$

Let $\phi_B(t)$ be the fundamental matrix solution of the system $\dot{x} = B(t)x$ with $\phi_B(0) = I$. By the comparison principle, it follows that $\phi(t) \geq \phi_B(t)$, and hence, $\phi(\omega) \geq \phi_B(\omega)$. Using [43, Theorem A.4], we then obtain

$$\rho = r(\phi(\omega)) \geq r(\phi_B(\omega)) = \max\{e^{\int_0^\omega (g_1(0,0,t) - D_1(t))dt}, e^{\int_0^\omega (g_2(0,t) - D_2(t))dt}\}.$$

In the case where (M1) holds, we have $\rho > 1$. ■

Lemma 2.2.2 *Solutions of (2.2) are uniformly bounded, in the sense that for any $b > 0$, there is $B(b) > 0$, such that $(x_1(t), x_2(t), y(t)) \in [0, B]^3$ if $(x_1(0), x_2(0), y(0)) \in$*

$[0, b]^3$. The solutions are also ultimately bounded, in the sense that there is N , such that $(x_1(t), x_2(t), y(t))$ lies in $[0, N]^3$ eventually.

Proof. Given $b > 0$, let $x(t) = (x_1(t), x_2(t), y(t))$ be the solution of (2.2) satisfying $x(0) \in [0, b]^3$. Let $B = \max\{b, M_1\}$, then $(x_1(t), x_2(t)) \in [0, B]^2$, $\forall t \geq 0$. By assumption (H2), there exists $N_1 = N_1(B) > 0$, such that $g_3(B, N_1, t) \leq 0$, $\forall t \in [0, \infty)$. Hence, let $\bar{N} = \max\{N_1, b\}$, we have $y(t) \in [0, \bar{N}]$, $\forall t \geq 0$. Thus, solutions of (2.2) are uniformly bounded. To prove the ultimate boundedness, we consider two cases. In the case where $\rho > 1$, Lemma 2.2.1 implies that there exists a unique positive ω -periodic solution $(x_1^*(t), x_2^*(t))$ of (2.5), and it is globally asymptotically stable in $\mathbb{R}_+^2 \setminus \{0\}$. Given a solution $(x_1(t), x_2(t), y(t))$ of system (2.2), we have

$$\begin{cases} \frac{dx_1(t)}{dt} \leq x_1 g_1(x_1, 0, t) + D_1(t)(x_2 - x_1) \\ \frac{dx_2(t)}{dt} \leq x_2 g_2(x_2, t) + D_2(t)(x_1 - x_2). \end{cases} \quad (2.7)$$

Let $(\bar{x}_1(t), \bar{x}_2(t))$ be the solution of (2.5) with $(\bar{x}_1(0), \bar{x}_2(0)) = (x_1(0), x_2(0))$. By the comparison theorem, we have $x_i(t) \leq \bar{x}_i(t)$, $i = 1, 2$. Fix $M > M_1$. Since $\lim_{t \rightarrow \infty} \bar{x}_i(t) = x_i^*(t)$, there exists $T > 0$ such that $x_i(t) \leq \bar{x}_i(t) \leq M$ for all $t \geq T$. Furthermore, there exists $N = N(M)$ such that $g_3(M, N, t) \leq 0$. Thus, $y(t) \leq N$ for all $t \geq T$. In the case where $\rho \leq 1$, Lemma 2.2.1 implies that every positive solution of (2.5) in $\mathbb{R}^2 \setminus \{0\}$ converges to $(0, 0)$. By a similar argument, we can show that solutions of (2.2) are ultimately bounded. Consequently, each solution $(x_1(t), x_2(t), y(t))$ satisfying $x_i(0) > 0, i = 1, 2, y(0) > 0$, lies eventually in the set $K_0 := \{(x_1, x_2, y) : 0 < x_i \leq M, i = 1, 2, 0 < y \leq N\}$. ■

Theorem 2.2.3 *Let (M1) hold, and let $(x_1^*(t), x_2^*(t))$ be the unique positive ω -periodic solution of system (2.4). Assume that*

$$(M2) \quad m(g_3(x_1^*(t), 0, t)) > 0.$$

Then system (2.2) is uniformly persistent in $\text{Int}(\mathbb{R}_+^3)$, and admits at least one positive periodic solution.

Proof. Let $S : X := \mathbb{R}_+^3 \rightarrow \mathbb{R}_+^3$ be the Poincaré map associated with (2.2), that is,

$$S(x_0) = u(\omega, x_0), \quad \forall x_0 \in \mathbb{R}_+^3,$$

where $u(\omega, x_0)$ is the solution of (2.2) with $u(0, x_0) = x_0$. Let $X_0 := \text{Int}(\mathbb{R}_+^3)$ and

$$W^s(M) := \{x \in X : \lim_{n \rightarrow \infty} d(S^n(u), M) = 0\}.$$

Obviously, $M_0 = (0, 0, 0)$ and $M_1 = (x_1^*(0), x_2^*(0), 0)$ are two fixed points of S . Define

$$\Sigma_1 := \{(x_1, 0, y) : x_1 > 0, y > 0\} \quad \text{and} \quad \Sigma_2 := \{(0, x_2, y) : x_2 > 0, y > 0\}.$$

We then claim that

$$M_\partial = \{(0, 0, y) : y \geq 0\} \cup \{(x_1, x_2, 0) : x_1 \geq 0, x_2 \geq 0\}.$$

Indeed, on Σ_1 and Σ_2 , we have $\dot{x}_2 = D_2(t)x_1 > 0$ and $\dot{x}_1 = D_1(t)x_2 > 0$, respectively.

Then $x(0) \in \Sigma_1 \cup \Sigma_2 \Rightarrow x(t) \in X_0$. Hence, $\Sigma_1 \cap M_\partial = \emptyset, \Sigma_2 \cap M_\partial = \emptyset$. Since

$$\phi(t, (0, 0, y(0))) = (0, 0, y(t)), \phi(t, (x_1(0), x_2(0), 0)) = (x_1(t), x_2(t), 0), \forall t \geq 0,$$

we obtain

$$\phi(t, \{0\} \times \{0\} \times \mathbb{R}_+) \subset \{0\} \times \{0\} \times \mathbb{R}_+, \phi(t, \mathbb{R}_+^2 \times \{0\}) \subset \mathbb{R}_+^2 \times \{0\}, \forall t \geq 0.$$

Letting $t = n\omega$, we have

$$\phi(n\omega, \{0\} \times \{0\} \times \mathbb{R}_+) \subset \{0\} \times \{0\} \times \mathbb{R}_+ \subset \partial X_0, \phi(n\omega, \mathbb{R}_+^2 \times \{0\}) \subset \mathbb{R}_+^2 \times \{0\} \subset \partial X_0.$$

This proves the claim. By our assumptions, we have $\int_0^\omega g_3(x_1^*(t), 0, t)dt > 0$, and either $\int_0^\omega (g_1(0, 0, t) - D_1(t))dt > 0$, or $\int_0^\omega (g_2(0, t)dt - D_2(t))dt > 0$. By Theorem 1.1.2, there exists $\delta_i > 0, i = 0, 1$, such that

$$\limsup_{n \rightarrow \infty} d(S^n(u), M_i) \geq \delta_i, u \in X_0, i = 0, 1,$$

which implies that M_i is isolated in X , and $W^s(M_i) \cap X_0 = \emptyset, i = 0, 1$. Note that $\int_0^\omega g_3(0, 0, t)dt \leq 0$. By Theorem 1.2.3 with $n = 1$, as applied to the Poincaré map associated with $\dot{y} = yg_3(0, y, t)$, it follows that any nonnegative solution $y(t)$ of $\dot{y} = yg_3(0, y, t)$ satisfies $\lim_{t \rightarrow \infty} y(t) = 0$, and hence, $S^n(0, 0, y(0)) = (0, 0, y(n\omega)) \rightarrow M_0$ as $n \rightarrow \infty$. Thus, we have

$$\Omega(M_\partial) := \cup_{x \in M_\partial} \omega(x) \subset M_0 \cup M_1.$$

It is easy to see that no subsets of $\{M_0, M_1\}$ can form a cycle in ∂X_0 . By Theorem 1.1.4, it follows that S is uniformly persistent, and hence, solutions of system (2.2) are uniformly persistent by Theorem 1.1.3. Moreover, Theorem 1.1.5 implies that S has a positive fixed point x_0 . Clearly, $u(t, x_0)$ is a positive periodic solution of (2.2).

■

By Theorem 2.2.3, we can choose $m, n, M, N > 0$, such that every positive solution eventually lies in the compact set

$$K_1 := \{(x_1, x_2, y) : m \leq x_i \leq M, i = 1, 2, n \leq y \leq N\}.$$

In order to obtain the uniqueness and global attractivity of periodic solution, we write system (2.2) as

$$\frac{dx_i}{dt} = x_i F_i(t, x), 1 \leq i \leq 3, \quad (2.8)$$

where $x = (x_1, x_2, x_3) \in X_0 = \text{Int}(\mathbb{R}_+^3)$, $F_1(t, x) = g_1(x_1, x_3, t) + D_1(t) \left(\frac{x_2}{x_1} - 1 \right)$, $F_2(t, x) = g_2(x_2, t) + D_2(t) \left(\frac{x_1}{x_2} - 1 \right)$, $F_3(t, x) = g_3(x_1, x_3, t)$. Then we have the following result.

Theorem 2.2.4 *Let (M1) and (M2) hold. Assume that*

(M3) There exist continuously differentiable functions $\beta_i : (0, \infty) \rightarrow (0, \infty)$, $1 \leq i \leq$

3, and a non-positive periodic function $b : \mathbb{R}_+ \rightarrow \mathbb{R}$ with $m(b) < 0$ such that

$$\frac{\partial(\beta_i(x_i)F_i(t, x))}{\partial x_i} + \sum_{j=1, j \neq i}^3 \beta_j(x_j) \left| \frac{\partial F_j(t, x)}{\partial x_i} \right| < b(t)$$

for all $t \in \mathbb{R}_+$, $x = (x_1, x_2, x_3) \in K_1$.

Then system (2.8) has a unique positive ω -periodic solution which is globally asymptotically stable in $\text{Int}(\mathbb{R}_+^3)$.

Proof. By Theorem 2.2.3, (2.8) has a positive ω -periodic solution $u(t) = (u_1(t), u_2(t), u_3(t))$.

Let $x(t) = (x_1(t), x_2(t), x_3(t))$ be any other solution of (2.8) with $x(0) \in X_0$. Thus,

$x(t)$ ultimately lies in K_1 . Without loss of generality, we assume that $x(t) \in K_1$,

$\forall t \geq 0$. Define

$$V(x, u) := \sum_{i=1}^3 \left| \int_{u_i}^{x_i} \frac{\beta_i(s)}{s} ds \right|, \quad \forall x, u \in K_1.$$

Since $\beta_i(s)/s > 0$, $\forall s > 0$, there exist c_1 and $c_2 \in (0, \infty)$ such that

$$c_1 \sum_{i=1}^3 |u_i - x_i| \leq V(x, u) \leq c_2 \sum_{i=1}^3 |u_i - x_i|, \quad \forall x, u \in K_1.$$

Let $p = rx + (1-r)u$, $r \in [0, 1]$. It then follows that

$$\begin{aligned} \frac{d}{dt} \int_{u_i(t)}^{x_i(t)} \frac{\beta_i(s)}{s} ds &= \beta_i(x_i(t)) F_i(t, x(t)) - \beta_i(u_i(t)) F_i(t, u(t)) \\ &= \int_0^1 \frac{d}{dr} (\beta_i(p_i) F_i(t, p)) dr \\ &= \int_0^1 \left[\frac{\partial (\beta_i(p_i) F_i(t, p))}{\partial p_i} (x_i - u_i) + \beta_i(p_i) \cdot \right. \\ &\quad \left. \sum_{j=1, j \neq i}^3 \frac{\partial F_i(t, p)}{\partial p_j} (x_j - u_j) \right] dr. \end{aligned}$$

Let $V(t) = V(x(t), u(t))$, and $D^+V(t)$ be the upper Dini derivative of $V(x(t), u(t))$

with respect to t . We then have

$$\begin{aligned} D^+V(t) &\leq \sum_{i=1}^3 \int_0^1 \left[\frac{\partial (\beta_i(p_i) F_i(t, p))}{\partial p_i} \cdot |x_i - u_i| + \beta_i(p_i) \cdot \sum_{j=1, j \neq i}^3 \left| \frac{\partial F_i(t, p)}{\partial p_j} \right| \cdot |x_j - u_j| \right] dr \\ &= \int_0^1 \left[\sum_{i=1}^3 \left(\frac{\partial (\beta_i(p_i) F_i(t, p))}{\partial p_i} + \sum_{j=1, j \neq i}^3 \beta_j(p_j) \left| \frac{\partial F_j(t, p)}{\partial p_i} \right| \right) |x_i - u_i| \right] dr \\ &\leq b(t) \sum_{i=1}^3 |x_i - u_i| \leq \frac{b(t)}{c_1} V(t). \end{aligned}$$

By the comparison theorem, we get

$$0 \leq V(t) \leq \left(e^{\int_0^t b(s) ds} \right)^{\frac{1}{c_1}} V(0).$$

Since $m(b) < 0$, we have $\lim_{t \rightarrow \infty} V(t) = 0$, which implies that $\lim_{t \rightarrow \infty} |x_i(t) - u_i(t)| = 0$, $i = 1, 2, 3$. Let $c_3 := \sup_{t \geq 0} \left\{ \left(e^{\int_0^t b(s) ds} \right)^{\frac{1}{c_1}} \right\}$. Since

$$c_1 \sum_{i=1}^3 |u_i(t) - x_i(t)| \leq V(t) \leq \left(e^{\int_0^t b(s) ds} \right)^{\frac{1}{c_1}} V(0) \leq c_3 V(0) \leq c_2 c_3 \sum_{i=1}^3 |u_i(0) - x_i(0)|,$$

it follows that $u(t)$ is Liapunov stable. ■

Remark 2.2.5 Letting $\beta_i \equiv 1, i = 1, 2, 3$, we have the following sufficient condition for (M3):

$$(M_4) \quad \frac{\partial g_1(x_1, x_3, t)}{\partial x_1} + \frac{\partial g_3(x_1, x_3, t)}{\partial x_1} - \frac{D_1 x_2}{x_1^2} + \frac{D_2}{x_2} < 0, \quad \frac{\partial g_2(x_2, t)}{\partial x_2} - \frac{D_2 x_1}{x_2^2} + \frac{D_1}{x_1} < 0,$$

$$\frac{\partial g_3(x_1, x_3, t)}{\partial x_3} - \frac{\partial g_1(x_1, x_3, t)}{\partial x_3} < 0, \quad \forall t \geq 0, x = (x_1, x_2, x_3) \in K_1.$$

Remark 2.2.6 Note that for system (2.1), (M4) reduces to

$$(M5) \quad b_1 > e - \frac{D_1 x_2}{x_1^2} + \frac{D_2}{x_2}, \quad b_2 > \frac{D_1}{x_1} - \frac{D_2 x_1}{x_2^2}, \quad q(t) > c(t).$$

For a continuous function $f(t)$, we define $f^U := \sup_{t \geq 0} \{f(t)\}$, $f^L := \inf_{t \geq 0} \{f(t)\}$. It is easy to see that the following condition is sufficient for (M4):

$$(M6) \quad b_1^L > e^U - \frac{D_1^L m}{M^2} + \frac{D_2^U}{m}, \quad b_2^L > \frac{D_1^U}{m} - \frac{D_2^L m}{M^2}, \quad q^L > c^U.$$

2.3 Global extinction and numerical simulations

In this section, we establish sufficient conditions for the global extinction of the predator species, and provide numerical simulation results.

Theorem 2.3.1 Let (M1) hold. Assume that

$$(M7) \quad m(g_3(x_1^*(t), 0, t)) < 0.$$

Then $(x_1^*(t), x_2^*(t), 0)$ is globally asymptotically stable in $\mathbb{R}_+^3 \setminus \{0\}$.

Proof. It suffices to prove that $(x_1^*(0), x_2^*(0), 0)$ is a globally asymptotically stable fixed point of S . By (M1) and Theorem 1.1.2, there exists $\delta_0 > 0$ such that

$$\limsup_{n \rightarrow \infty} d(S^n(u), (0, 0, 0)) \geq \delta_0, \quad \forall u \in X_0.$$

Then $(0, 0, 0)$ is an isolated invariant set for S in X , and $X_0 \cap W^s((0, 0, 0)) = \emptyset$. By (M7), we can choose $0 < \epsilon \ll 1$ such that $m(g_3(x_1^*(t) + \epsilon, 0, t)) < 0$. Let $(x_1(t), x_2(t), y(t))$ be a given solution of (2.2) with $(x_1(0), x_2(0), y(0)) \in X_0$. As argued in the proof of Lemma 2.2.2, there exists $T > 0$ such that $x_1(t) \leq \bar{x}_1(t) \leq x_1^*(t) + \epsilon$ as $t \geq T$. Thus we have $\dot{y} \leq yg_3(x_1^*(t) + \epsilon, y, t), \forall t \geq T$. By Theorem 1.2.3 with $n = 1$, as applied to the Poincaré map associated with $\dot{y} = yg_3(x_1^*(t) + \epsilon, y, t)$, it follows that any nonnegative solution $\bar{y}(t)$ of $\dot{y} = yg_3(x_1^*(t) + \epsilon, y, t)$ satisfies $\lim_{t \rightarrow \infty} \bar{y}(t) = 0$. By the standard comparison method, we see that $\lim_{t \rightarrow \infty} y(t) = 0$. For convenience, we write $\omega(x_1(0), x_2(0), y(0)) = \omega_1 \times \{0\}$, where $(x_1(0), x_2(0), y(0)) \in X_0$. Note that $\omega(x_1(0), x_2(0), y(0))$ is a compact internally chain-transitive set for S . It follows that ω_1 is a compact internally chain-transitive set for $S_1 : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$, where S_1 is the Poincaré map associated with (2.4). Let

$$W^s(x_1^*(0), x_2^*(0)) := \{(x_1, x_2) : S_1^n(x_1, x_2) \rightarrow (x_1^*(0), x_2^*(0)) \text{ as } n \rightarrow \infty\}.$$

We further claim that $\omega_1 \cap W^s(x_1^*(0), x_2^*(0)) \neq \emptyset$. Assume, by contradiction, that $\omega_1 \cap W^s(x_1^*(0), x_2^*(0)) = \emptyset$. Then $\omega_1 = (0, 0)$, and hence, $\omega(x_1(0), x_2(0), y(0)) =$

$(0, 0, 0)$. Thus, we have $(x_1(0), x_2(0), y(0)) \in W^s(0, 0, 0)$, which contradicts the fact that $X_0 \cap W^s((0, 0, 0)) = \emptyset$. Since $\omega_1 \cap W^s(x_1^*(0), x_2^*(0)) \neq \emptyset$, Theorem 1.1.11 implies that $\omega_1 = (x_1^*(0), x_2^*(0))$. Thus, $\omega(x_1(0), x_2(0), y(0)) = (x_1^*(0), x_2^*(0), 0)$, which proves that $(x_1^*(0), x_2^*(0), 0)$ is globally attractive in $\mathbb{R}_+^3 \setminus \{0\}$.

It remains to prove the stability of $(x_1^*(t), x_2^*(t), 0)$ for (2.2). For simplicity, we write the system (2.2) as

$$\frac{dx}{dt} = G(t, x), \quad (2.9)$$

where $x = (x_1, x_2, y)$, $G(t, x) = (G_1(t, x), G_2(t, x), G_3(t, x))$ with

$$G_1(t, x) = x_1 g_1(x_1, y, t) + D_1(t)(x_2 - x_1),$$

$$G_2(t, x) = x_2 g_2(x_2, t) + D_2(t)(x_1 - x_2),$$

$$G_3(t, x) = y g_3(x_1, y, t).$$

Let $x^*(t) = (x_1^*(t), x_2^*(t), 0)$. Note that $D_x G(t, x^*(t)) =$

$$\begin{pmatrix} g_1(x_1, 0, t) + x_1 \frac{\partial g_1}{\partial x_1} - D_1(t) & D_1(t) & x_1 \frac{\partial g_1}{\partial y} \big|_{y=0} \\ D_2(t) & g_2(x_2, t) + x_2 \frac{\partial g_2}{\partial x_2} - D_2(t) & 0 \\ 0 & 0 & g_3(x_1, 0, t) \end{pmatrix} \bigg|_{\substack{x_1=x_1^*(t) \\ x_2=x_2^*(t)}}$$

It then follows that

$$\Phi_{D_x G(t, x^*(t))}(t) \begin{pmatrix} x_1(0) \\ x_2(0) \\ y(0) \end{pmatrix} = \begin{pmatrix} \Phi_{A_1}(t) \begin{pmatrix} x_1(0) \\ x_2(0) \end{pmatrix} & H(t) \\ 0 & \Phi_{A_2}(t) y_0 \end{pmatrix}$$

with

$$A_1(t) = \begin{pmatrix} g_1(x_1, 0, t) + x_1 \frac{\partial g_1}{\partial x_1} - D_1(t) & D_1(t) \\ D_2(t) & g_2(x_2, t) + x_2 \frac{\partial g_2}{\partial x_2} - D_2(t) \end{pmatrix}_{\substack{x_1=x_1^*(t), \\ x_2=x_2^*(t)}},$$

$$A_2(t) = g_3(x_1^*(t), 0, t),$$

$$\begin{aligned} H(t) &= \begin{pmatrix} H_1(t) \\ H_2(t) \end{pmatrix} = \int_0^t \Phi_{A_1}(t-s) \begin{pmatrix} x_1^*(t) \frac{\partial g_1(x_1^*(t), 0, t)}{\partial y} \Phi_{A_2}(s) y(0) \\ 0 \end{pmatrix} ds \\ &= y(0) \begin{pmatrix} \int_0^t \Phi_{A_1}^{11}(t-s) x_1^*(t) \frac{\partial g_1(x_1^*(t), 0, t)}{\partial y} \Phi_{A_2}(s) ds \\ \int_0^t \Phi_{A_1}^{21}(t-s) x_1^*(t) \frac{\partial g_1(x_1^*(t), 0, t)}{\partial y} \Phi_{A_2}(s) ds \end{pmatrix} \\ &:= y(0) \begin{pmatrix} \bar{H}_1(t) \\ \bar{H}_2(t) \end{pmatrix} = y(0) \bar{H}(t), \end{aligned}$$

where $\Phi_{A_1}^{ij}(t-s)$ denotes the i th row and j th column element of the matrix $\Phi_{A_1}(t-s)$.

It follows that

$$\Phi_{D_x G(t, x^*(t))}(\omega) = \begin{pmatrix} \Phi_{A_1}(\omega) & \bar{H}(\omega) \\ 0 & \Phi_{A_2}(\omega) \end{pmatrix}.$$

Therefore, $r(\phi_{D_x G(t, x^*(t))}(\omega)) = \max\{r(\phi_{A_1}(\omega)), r(\phi_{A_2}(\omega))\}$. Since

$$A_1(t) \leq \begin{pmatrix} g_1(x_1^*(t), 0, t) - D_1(t) & D_1(t) \\ D_2(t) & g_2(x_2^*(t), t) - D_2(t) \end{pmatrix} := A_3(t),$$

the comparison principle implies that $\phi_{A_1}(t) \leq \phi_{A_3}(t)$, and hence $\phi_{A_1}(\omega) \leq \phi_{A_3}(\omega)$.

By [43, Theorem A.4], we have $r(\phi_{A_1}(\omega)) < r(\phi_{A_3}(\omega))$. Since

$$\phi_{A_3}(t) \begin{pmatrix} x_1^*(0) \\ x_2^*(0) \end{pmatrix} = \begin{pmatrix} x_1^*(t) \\ x_2^*(t) \end{pmatrix},$$

It follows that

$$\phi_{A_3}(\omega) \begin{pmatrix} x_1^*(0) \\ x_2^*(0) \end{pmatrix} = \begin{pmatrix} x_1^*(\omega) \\ x_2^*(\omega) \end{pmatrix} = \begin{pmatrix} x_1^*(0) \\ x_2^*(0) \end{pmatrix},$$

and hence, $r(\phi_{A_3}(\omega)) = 1$. Consequently,

$$r(\phi_{D_x G(t, x^*(t))}(\omega)) = \max\{r(\phi_{A_1}(\omega)), e^{\int_0^\omega g_3(x_1^*(t), 0, t) dt}\} < 1,$$

which implies the stability of $(x_1^*(t), x_2^*(t), 0)$. ■

In order to simulate the global coexistence, we consider the following system

$$\begin{cases} \frac{dx_1}{dt} = x_1(21 - 7x_1 - y) + (8 + \sin t)(x_2 - x_1) \\ \frac{dx_2}{dt} = x_2(10 - 5x_2) + \left(\frac{1}{3} + \frac{1}{6} \sin t\right)(x_1 - x_2) \\ \frac{dy}{dt} = y(-11 + 6x_1 - 7y). \end{cases} \quad (2.10)$$

We then get a compact region

$$K_1 := \{(x_1, x_2, y) : 2 \leq x_i \leq 3, i = 1, 2, 1/7 \leq y \leq 1\}$$

such that for each solution $(x_1(t), x_2(t), y(t))$ satisfying $x_i(0) > 0, i = 1, 2, y(0) > 0$, there exists $\bar{T}_1 > 0$ such that $(x_1(t), x_2(t), y(t)) \in K_1$ for $t \geq \bar{T}_1$. It is easy to verify

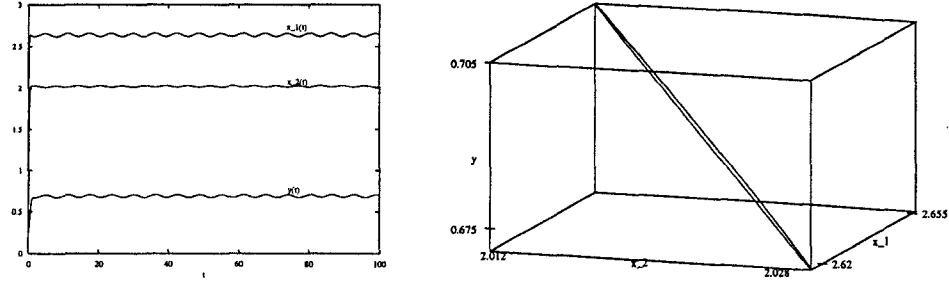


Figure 2.1: The solution of system

(2.10): Global coexistence

that conditions (M1), (M2) and (M4) are satisfied. By Theorem 2.2.4, system (2.10) has a unique positive 2π -periodic solution, which is globally asymptotically stable in $\text{Int}(\mathbb{R}_+^3)$. Our numerical simulations in Figure 2.1 confirm this result.

Regarding the global extinction, we modify system (2.10) into the following one:

$$\begin{cases} \frac{dx_1}{dt} = x_1(21 - 7x_1 - y) + (8 + \sin t)(x_2 - x_1) \\ \frac{dx_2}{dt} = x_2(10 - 5x_2) + \left(\frac{1}{3} + \frac{1}{6} \sin t\right)(x_1 - x_2) \\ \frac{dy}{dt} = y(-11 + 10x_1 - 16y). \end{cases} \quad (2.11)$$

Thus, we get a compact region

$$K_2 = \{(x_1, x_2, y) : 2 \leq x_i \leq 3, i = 1, 2, 0 \leq y \leq 1\}$$

such that for each solution $(x_1(t), x_2(t), y(t))$ with $x_i(0) > 0, i = 1, 2, y(0) \geq 0$, there exists $\bar{T}_2 > 0$ such that $(x_1(t), x_2(t), y(t)) \in K_2$ for $t \geq \bar{T}_2$. It is easy to verify that the conditions (M1) and (M7) are satisfied for (2.11). By Theorem 2.3.1, $(x_1^*(t), x_2^*(t), 0)$ is globally asymptotically stable. Our numerical simulations in Figure 2.2 are consistent with this result.

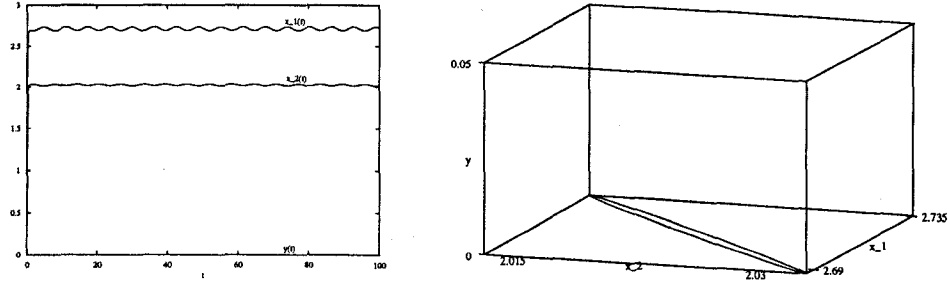


Figure 2.2: The solution of system

(2.11): Global extinction

2.4 Asymptotically periodic case

In this section, we will extend the results in Sections 2.2 and 2.3 to the asymptotically periodic system (2.3).

Let $\Phi : \Delta_0 \times X \rightarrow X$, $\Delta_0 = \{(t, s) : 0 \leq s \leq t < \infty\}$, be the nonautonomous semiflow associated with system (2.3), and $T(t) : X \rightarrow X, t \geq 0$, the ω -periodic semiflow associated with system (2.2). The assumption (H3) implies that

$$\Phi(t_j + n_j\omega, n_j\omega, x_j) \rightarrow T(t)x \quad \text{as } j \rightarrow \infty,$$

for any three sequences $t_j \rightarrow t$, $n_j \rightarrow \infty$, $x_j \rightarrow x$ with $x, x_j \in X$. Thus, Φ is an asymptotically periodic semiflow with limit ω -periodic semiflow $T(t) : X \rightarrow X, t \geq 0$. Define $T_n(x) := \Phi(n\omega, 0, x), \forall n \in N, x \in X$. Then $T_n : X \rightarrow X$ is an asymptotically autonomous discrete process with limit autonomous discrete semiflow $S : X \rightarrow X$. By Lemma 2.2.2, we see that solutions of (2.3) are uniformly bounded. We further have the following three results on the long-term behavior of solutions of (2.3).

Theorem 2.4.1 *Let (M1) and (M2) hold. Then system (2.3) is uniformly persistent in $Int(\mathbb{R}_+^3)$.*

Proof. For each $i = 0, 1$, let

$$\tilde{W}^s(M_i) = \{x \in \mathbb{R}_+^3 : \lim_{n \rightarrow \infty} T_n(x) = M_i\}.$$

By [16, Theorem 5.1.2], it then follows that $\tilde{W}^s(M_i) \cap X_0 = \emptyset$, $i = 0, 1$. Let $\tilde{\omega}(x)$ be the omega limit set of any precompact orbit of $T_n(x)$, $x \in X_0$. By Theorem 1.1.10, $\tilde{\omega}(x)$ is a compact internally chain transitive set for S^n . Now we show that $\tilde{\omega}(x) \not\subset M_i$, $i = 0, 1$. Assume, by contradiction, that $\tilde{\omega}(x) \subset M_i$ for some i and $x \in X_0$. Then $T_n(x) \rightarrow M_i$ as $n \rightarrow \infty$, and hence, $x \in \tilde{W}^s(M_i) \cap X_0$, a contradiction. By Theorem 1.1.4, it then follows that there exists $\delta > 0$ such that $\inf_{y \in \tilde{\omega}(x)} d(y, \partial X_0) \geq \delta$. Let A_0 be the global attractor for $S : X_0 \rightarrow X_0$. Then $\tilde{\omega}(x) \subset X_0$, and hence $\tilde{\omega}(x) \subset A_0$. Therefore, $T_n(x) \rightarrow A_0$, that is, $\lim_{n \rightarrow \infty} d(T_n(x), A_0) = 0$. Let $\tilde{A} = \cup_{t \geq 0} T(t)A_0 \subset X_0$. By [63, Theorem 3.2.1], it follows that $\lim_{t \rightarrow \infty} d(\phi(t, 0, x), \tilde{A}) = 0$, which implies the uniform persistence of the solution $\phi(t, 0, x)$, $x \in X_0$, of system (2.3). ■

Theorem 2.4.2 *Assume that (M1), (M2) and (M3) hold, and let $(u_1(t), u_2(t), v(t))$ be the unique positive ω -periodic solution of (2.2). Then every solution of (2.3) in $Int(\mathbb{R}_+^3)$ is asymptotic to $(u_1(t), u_2(t), v(t))$.*

Proof. By Theorem 2.2.4, $(u_1(0), u_2(0), v(0))$ is a global attractor for S in X_0 . Let $x \in X_0$ be fixed. Then $\tilde{\omega}(x)$ is internally chain transitive for S . As mentioned in

the proof of Theorem 2.4.1, $\tilde{W}^s(M_i) \cap X_0 = \emptyset, i = 0, 1$. We now claim that $\tilde{\omega}(x) \cap W^s(u_1(0), u_2(0), v(0)) \neq \emptyset$. Otherwise, we have

$$\tilde{\omega}(x) \subset \Sigma := \{(x_1, x_2, 0) : x_1 \geq 0, x_2 \geq 0\} \cup \{(0, 0, y) : y \geq 0\}.$$

Applying the convergence Theorem 1.1.12 to $S|_\Sigma : \Sigma \rightarrow \Sigma$, we have either $\tilde{\omega}(x) = M_0$, or $\tilde{\omega}(x) = M_1$, which contradicts $\tilde{W}^s(M_i) \cap X_0 = \emptyset, i = 0, 1$. By Theorem 1.1.11, we then have $\tilde{\omega}(x) = (u_1(0), u_2(0), v(0))$, and hence, [63, Theorem 3.2.1] implies that $\|\phi(t, 0, x) - (u_1(t), u_2(t), v(t))\| \rightarrow 0$ as $t \rightarrow \infty$. ■

Theorem 2.4.3 *Let (M1) and (M7) hold. Then every solution of (2.3) in $\text{Int}(\mathbb{R}_+^3)$ is asymptotic to $(x_1^*(t), x_2^*(t), 0)$.*

Proof. By Theorem 2.3.1, $(x_1^*(0), x_2^*(0), 0)$ is a global attractor for S in X_0 . Let $x \in X_0$ be fixed. Then $\tilde{\omega}(x)$ is internally chain-transitive for S . Note that

$$W^s(x_1^*(0), x_2^*(0), 0) = X \setminus \{(0, 0, y) : y \geq 0\}.$$

We claim that $\tilde{\omega}(x) \cap W^s(x_1^*(0), x_2^*(0), 0) \neq \emptyset$. Otherwise, $\tilde{\omega}(x) \subset \{(0, 0, y) : y \geq 0\}$. Hence, $\tilde{\omega}(x) = (0, 0, 0)$, which contradicts the fact that $W^s(M_0) \cap X_0 = \emptyset$. By Theorem 1.1.11, we have $\tilde{\omega}(x) = (x_1^*(0), x_2^*(0), 0)$, and hence, every solution of (2.3) in X_0 is asymptotic to $(x_1^*(t), x_2^*(t), 0)$. ■

Finally, we should point out that Cui, Takeuchi and Lin [9] studied the permanence

and extinction of the following dispersal population systems,

$$\left\{ \begin{array}{l} \frac{dx_1}{dt} = x_1(a_1(t) - b_1(t)x_1 - \phi(t, x_1)y) + \sum_{j=1}^n (D_{1j}(t)x_j - D_{j1}(t)x_1) \\ \frac{dx_i}{dt} = x_i(a_i(t) - b_i(t)x_i) + \sum_{j=1}^n (D_{ij}(t)x_j - D_{ji}(t)x_i), \quad 2 \leq i \leq n, \\ \frac{dy}{dt} = y(-d(t) + e(t)x_1\phi(t, x_1) - q(t)y). \end{array} \right. \quad (2.12)$$

Note that system (2.12) with $n = 2$ and $D_{12} = D_{21}$ is a special case of our model with $D_1 = D_2$. Our sufficient conditions for permanence and global extinction are similar to those in [6]. However, the existence, uniqueness and global attractivity of positive periodic solution and the asymptotically periodic case were not discussed in [9]. Furthermore, our dynamical systems approach may also apply to the analysis of system (2.12).

Chapter 3

A Periodic Epidemic Model

An epidemic model in a patchy environment with periodic coefficients is investigated in this chapter. By employing the persistence theory, we establish a threshold between the extinction and the uniform persistence of the disease. Further, we obtain the conditions under which the positive periodic solution is globally asymptotically stable. At last, we present two examples and numerical simulations.

This chapter is organized as follows. In Section 3.1, we present the model and introduce some related work. In Section 3.2, a threshold between the extinction and persistence of the disease is established. In Section 3.3, we prove the uniqueness and the global asymptotic stability of the positive periodic solution when susceptible and infectious individuals have the same dispersal rates, and the global attractivity of the positive periodic solution when the dispersal rates of susceptible and infectious individuals are very close. Finally, we present numerical simulations for the model with two patches.

3.1 Introduction

The study of the threshold that determines the persistence and extinction of infectious diseases is one of the most important subjects in mathematical epidemiology. An extensive literature have dealt with the threshold conditions of many different kinds of epidemic models. The reproduction numbers for a series of epidemic models have been studied by many mathematicians(see, e.g., [13, 14, 26, 48, 8, 15, 16] and references therein).

It has been observed that population dispersal affects the spread of many infectious diseases. In 1976, Hethcote [22] put forth an epidemic model with population dispersal between two patches. After him, Brauer and van den Driessche [3] proposed a model with immigration of infectives. In [51], Wang and Zhao presented a disease transmission model with population dispersal among n patches,

$$\begin{cases} S'_i = B_i(N_i)N_i - \mu_i S_i - \beta_i S_i I_i + \gamma_i I_i + \sum_{j=1}^n a_{ij} S_j, & 1 \leq i \leq n, \\ I'_i = \beta_i S_i I_i - (\mu_i + \gamma_i) I_i + \sum_{j=1}^n b_{ij} I_j, & 1 \leq i \leq n, \end{cases} \quad (3.1.1)$$

with the properties

$$\sum_{j=1}^n a_{ji} = 0, \quad \sum_{j=1}^n b_{ji} = 0, \quad \forall 1 \leq i \leq n, \quad (3.1.2)$$

and established a threshold between the extinction and the uniform persistence of the disease for this model. They also considered the global attractivity of the disease-free equilibrium under the condition that the dispersal rates of susceptible and infective

individuals are the same in each patch. Moreover, the uniqueness and the global attractivity of the endemic equilibrium of this model has been studied by Jin and Wang [28]. Recently, Wang and Zhao [52] incorporated an age structure into their model in order to simulate the phenomenon that some diseases only occur in the adult population. They established sufficient conditions for global extinction and uniform persistence. However, these authors only considered constant coefficients in model (3.1.1). Since periodicity has been observed in the incidence of many infectious diseases, such as measles, chickenpox, mumps, rubella, poliomyelitis, diphtheria, pertussis and influenza (see, e.g., [23]), it is more realistic to assume that all the coefficients depend on time periodically. As mentioned in [12] and [35], the seasonality is an important factor for the spread of infectious diseases, such as the marked change of the contact rate caused by the school system or the weather changes (e.g., measles), the emergence of the insects caused by the seasonal variation (e.g., temperature, humidity, etc.). We will assume that these coefficients are periodic with a common period due to the seasonal effects.

In this chapter, we consider the periodic system

$$\begin{cases} S'_i = B_i(t, N_i)N_i - \mu_i(t)S_i - \beta_i(t)S_iI_i + \gamma_i(t)I_i + \sum_{j=1}^n a_{ij}(t)S_j, & 1 \leq i \leq n, \\ I'_i = \beta_i(t)S_iI_i - (\mu_i(t) + \gamma_i(t))I_i + \sum_{j=1}^n b_{ij}(t)I_j, & 1 \leq i \leq n, \end{cases} \quad (3.1.3)$$

with all functions being continuous and ω -periodic in t . Here S_i, I_i are the numbers of susceptible and infectious individuals in patch i , respectively. $N_i = S_i + I_i$ is the

number of the population in patch i , $B_i(t, N_i)$ is the birth rate of the population in the i th patch, $\mu_i(t)$ is the death rate of the population in the i th patch, and $\gamma_i(t)$ is the recovery rate of infectious individuals in the i th patch. $-a_{ii}(t), -b_{ii}(t) \geq 0$ represent the emigration rates of susceptible and infectious individuals in the i th patch, respectively. $a_{ij}(t), b_{ij}(t), j \neq i$, represent the immigration rates of susceptible and infectious individuals from j th patch to i th patch. Since the death rates and birth rates of the individuals during the dispersal process are ignored in this model, we have

$$\sum_{j=1}^n a_{ji}(t) = 0, \quad \sum_{j=1}^n b_{ji}(t) = 0, \quad \forall 1 \leq i \leq n, \quad \forall t \in [0, \omega]. \quad (3.1.4)$$

We further assume that

(H1) $a_{ij}(t) \geq 0, b_{ij}(t) \geq 0, a_{ii}(t) \leq 0, b_{ii}(t) \leq 0, \forall 1 \leq i \neq j \leq n, t \in [0, \omega]$, and the two $n \times n$ matrices $(a_{ij}(t))$ and $(b_{ij}(t))$ are irreducible.

(H2) $B_i(t, N_i) > 0, \forall (t, N_i) \in \mathbb{R}_+ \times (0, \infty), 1 \leq i \leq n$.

(H3) $B_i(t, N_i)$ is continuously differentiable with $\frac{\partial B_i(t, N_i)}{\partial N_i} < 0, \forall (t, N_i) \in \mathbb{R}_+ \times (0, \infty), 1 \leq i \leq n$.

(H4) $B_i^u(\infty) := \lim_{N_i \rightarrow \infty} B_i^u(N_i) < \mu_i^l, 1 \leq i \leq n$, where $B_i^u(N_i) := \max_{t \in [0, \omega]} B_i(t, N_i)$, $\mu_i^l := \min_{t \in [0, \omega]} \mu_i(t)$.

Biologically, (H1) implies that these n patches cannot be separated into two groups such that there is no immigration of susceptible and infective individuals from first group to second group (see the definition of irreducibility in Section 3.2); (H2) and

(H3) mean that each birth rate function is positive and decreasing; and (H4) represents the case where each birth rate cannot exceed the death rate when the population number is sufficiently large.

3.2 Threshold dynamics

Let $(\mathbb{R}^k, \mathbb{R}_+^k)$ be the standard ordered k -dimensional Euclidean space with a norm $\|\cdot\|$. For $u, v \in \mathbb{R}^k$, we write $u \geq v$ provided $u - v \in \mathbb{R}_+^k$, $u > v$ provided $u - v \in \mathbb{R}_+^k \setminus \{0\}$, and $u \gg v$ provided $u - v \in \text{Int}(\mathbb{R}_+^k)$.

Recall that a $k \times k$ matrix (a_{ij}) is said to be cooperative if all of its off-diagonal entries are non-negative; irreducible if its index set $\{1, 2, \dots, k\}$ cannot be split into two complementary sets (without common indices) $\{m_1, m_2, \dots, m_\mu\}$ and $\{n_1, n_2, \dots, n_\nu\}$ ($\mu + \nu = k$) such that $a_{m_p n_q} = 0$, $\forall 1 \leq p \leq \mu, 1 \leq q \leq \nu$.

Let $A(t)$ be a continuous, cooperative, irreducible, and ω -periodic $k \times k$ matrix function, $\Phi_{A(\cdot)}(t)$ be the fundamental solution matrix of the linear ordinary differential system $x' = A(t)x$, and $r(\Phi_{A(\cdot)}(\omega))$ be the spectral radius of $\Phi_{A(\cdot)}(\omega)$. It then follows from [1, Lemma 2] (see also [24, Theorem 1.1]) that $\Phi_{A(\cdot)}(t)$ is a matrix with all entries positive for each $t > 0$. By the Perron-Frobenius theorem, $r(\Phi_{A(\cdot)}(\omega))$ is the principal eigenvalue of $\Phi_{A(\cdot)}(\omega)$ in the sense that it is simple and admits an eigenvector $v^* \gg 0$. The following result is useful for our subsequent comparison arguments.

Lemma 3.2.1 *Let $\mu = \frac{1}{\omega} \ln r(\Phi_{A(\cdot)}(\omega))$. Then there exists a positive, ω -periodic function $v(t)$ such that $e^{\mu t} v(t)$ is a solution of $x' = A(t)x$.*

Proof. Let $v^* \gg 0$ be an eigenvector associated with the principal eigenvalue $r(\Phi_{A(\cdot)}(\omega))$. By the change of variable $x(t) = e^{\mu t}v(t)$, we reduce the linear system $x' = A(t)x$ to

$$v' = A(t)v - \mu v = (A(t) - \mu I)v. \quad (3.2.5)$$

Thus, $v(t) := \Phi_{(A(\cdot) - \mu I)}(t)v^*$ is a positive solution of (3.2.5). It is easy to see that $e^{\mu t}\Phi_{(A(\cdot) - \mu I)}(t) = \Phi_{A(\cdot)}(t)$. Moreover,

$$v(\omega) = \Phi_{(A(\cdot) - \mu I)}(\omega)v^* = e^{-\mu\omega}\Phi_{A(\cdot)}(\omega)v^* = e^{-\mu\omega}r(\Phi_{A(\cdot)}(\omega))v^* = v^* = v(0).$$

Thus, $v(t)$ is a positive ω -periodic solution of (3.2.5), and hence, $x(t) = e^{\mu t}v(t)$ is a solution of $x' = A(t)x$. ■

Let $P : \mathbb{R}_+^{2n} \rightarrow \mathbb{R}_+^{2n}$ be the Poincaré map associated with (3.1.3), that is,

$$P(x^0) = u(\omega, x^0), \quad \forall x^0 \in \mathbb{R}_+^{2n},$$

where $u(t, x^0)$ is the unique solution of (3.1.3) with $u(0, x^0) = x^0$. In order to find the disease-free periodic solutions of (3.1.3), we consider

$$S'_i = B_i(t, S_i)S_i - \mu_i(t)S_i + \sum_{j=1}^n a_{ij}(t)S_j, \quad 1 \leq i \leq n. \quad (3.2.6)$$

Let $P_1 : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ be the Poincaré map associated with (3.2.6), that is,

$$P_1(S^0) = u_1(\omega, S^0), \quad \forall S^0 \in \mathbb{R}_+^n,$$

where $u_1(t, S^0)$ is the solution of (3.2.6) with $u_1(0, S^0) = S^0$.

If z is a nonnegative constant, we define an auxiliary matrix

$$M(t, z) := \begin{bmatrix} B_1(t, z) - \mu_1(t) + a_{11}(t) & \cdots & a_{1n}(t) \\ a_{21}(t) & \cdots & a_{2n}(t) \\ \vdots & \ddots & \vdots \\ a_{n1}(t) & \cdots & B_n(t, z) - \mu_n(t) + a_{nn}(t) \end{bmatrix}.$$

This matrix will be used to prove the existence and the uniqueness of a positive fixed point of P_1 and is different from the standard Jacobian matrix.

Let $F : \mathbb{R}_+^1 \times \mathbb{R}_+^n \rightarrow \mathbb{R}^n$ be defined by the right-hand side of (3.2.6). It is easy to see that F has the following properties:

(M1) $F_i(t, S) \geq 0$ for every $S \geq 0$ with $S_i = 0$, $t \in \mathbb{R}_+^1, 1 \leq i \leq n$;

(M2) $\frac{\partial F_i}{\partial S_j} \geq 0, i \neq j, \forall (t, S) \in \mathbb{R}_+^1 \times \mathbb{R}_+^n$, and $D_S F(t, 0)$ is irreducible for each $t \in \mathbb{R}_+^1, S \in \mathbb{R}_+^n$;

(M3) For each $t \geq 0$, $F(t, \cdot)$ is strictly subhomogeneous on \mathbb{R}_+^n in the sense that

$$F(t, \alpha S) > \alpha F(t, S), \forall S \gg 0, \alpha \in (0, 1);$$

(M4) $F(t, 0) \equiv 0$, and $F(t, S) < D_S F(t, 0)S, \forall t \geq 0, S \gg 0$.

Note that the nonlinear system (3.2.6) is dominated by the linear system $S' = D_S F(t, 0)S$. It then follows that for any $S^0 \in \mathbb{R}_+^n$, the unique solution $u_1(t, S^0)$ of (3.2.6) satisfying $u_1(0, S^0) = S^0$ exists globally on $[0, \infty)$ and $u_1(t, S^0) \geq 0, \forall t \geq 0$. We claim that (3.2.6) admits a bounded positive solution. Indeed, in view of (H4), we can choose a sufficient large real number K such that $\int_0^\omega (\mu_i(t) - B_i(t, K))dt >$

$0, i = 1, \dots, n$. Then by Lemma 3.2.1, there is a positive, ω -periodic function $v(t) = (v_1(t), v_2(t), \dots, v_n(t))$ such that $V(t) = e^{\bar{\mu}t}v(t)$ is a solution of $V' = M(t, K)V$, where $\bar{\mu} = \frac{1}{\omega} \ln r(\Phi_{M(\cdot, K)}(\omega))$. Let $\Sigma(t) = \sum_{i=1}^n V_i(t) = e^{\bar{\mu}t} \sum_{i=1}^n v_i(t)$. By the first equation in (3.1.4), it easily follows that $\Sigma'(t) \leq a(t)\Sigma(t)$, $\forall t \geq 0$, where $a(t) = \max\{B_i(t, K) - \mu_i(t) : 1 \leq i \leq n\}$. Thus, $\lim_{t \rightarrow \infty} \Sigma(t) = 0$, and hence $\bar{\mu} < 0$, i.e., $r(\Phi_{M(\cdot, K)}(\omega)) < 1$. Choose $l > 0$ large enough such that $lv_i(t) > K, 1 \leq i \leq n, \forall t \in [0, \omega]$. Set $H(t) \equiv lv(t)$. If we rewrite (3.2.6) as $S' = F(t, S)$, it is easy to see that

$$F(t, H(t)) < M(t, K)H(t), \quad \forall t \geq 0, \quad (3.2.7)$$

where (H3) is used. By the standard comparison theorem (see, e.g., [43, Theorem B.1]), it follows that

$$\begin{aligned} 0 < u_1(m\omega, lv(0)) &\leq \Phi_{M(\cdot, K)}(m\omega)lv(0) = r(\Phi_{M(\cdot, K)}(m\omega))lv(0) \\ &= r(\Phi_{M(\cdot, K)}(\omega))^m lv(0) < lv(0), \quad \forall m \geq 0. \end{aligned}$$

that is, $P_1^m(lv(0)) < lv(0), \forall m \geq 0$. Consequently, $P_1^m(lv(0))$ is bounded. In order for P_1 to admit a positive fixed point, we need to assume that

$$(H5) \quad r(\Phi_{M(\cdot, 0)}(\omega)) > 1.$$

By [63, Theorem 2.1.2], it then follows that the Poincaré map P_1 has a unique positive fixed point $S^* = (S_1^*, S_2^*, \dots, S_n^*)$ which is globally attractive for $S^0 \in \mathbb{R}_+^n \setminus \{0\}$. Thus, $E_0 = (S_1^*, S_2^*, \dots, S_n^*, 0, \dots, 0)$ is the unique disease-free fixed point of the Poincaré map P .

To investigate the global dynamics of (3.1.3), we first show that (3.1.3) admits a family of compact, positively invariant sets. For convenience, we denote the positive solution $(S_1(t), \dots, S_n(t), I_1(t), \dots, I_n(t))$ of (3.1.3) by $(S(t), I(t))$.

Lemma 3.2.2 *Let (H1)-(H5) hold. Then there is an $N^* > 0$ such that every forward solution in \mathbb{R}_+^{2n} of (3.1.3) eventually enters into $G_{N^*} := \{(S, I) \in \mathbb{R}_+^{2n} : \sum_{i=1}^n (S_i + I_i) \leq N^*\}$, and for each $N \geq N^*$, G_N is positively invariant for (3.1.3).*

Proof. Let $N = \sum_{i=1}^n N_i$, $N_i = S_i + I_i$. By (3.1.3) and (3.1.4), we have

$$N' = \sum_{i=1}^n (B_i(t, N_i) - \mu_i(t)) N_i \leq \sum_{i=1}^n (B_i^u(N_i) - \mu_i^l) N_i. \quad (3.2.8)$$

If $B_i^u(0+) := \lim_{N_i \rightarrow 0+} B_i^u(N_i) < \mu_i^l$, $i = 1, 2, \dots, n$, then there exists an $\alpha > 0$ such that $N'(t) \leq -\alpha N(t)$, $\forall t \geq 0$, and hence, Lemma 3.2.2 holds for any positive number N^* .

Otherwise, we partition $\{1, 2, \dots, n\}$ into two sets P_1 and P_2 such that

$$B_i^u(0+) > \mu_i^l, \quad \forall i \in P_1$$

$$B_i^u(0+) \leq \mu_i^l, \quad \forall i \in P_2.$$

Without loss of generality, we suppose that $P_1 = \{1, \dots, m\}$ and $P_2 = \{m+1, \dots, n\}$.

For $i \in P_1$, since $B_i^u(0+) > \mu_i^l$ and $B_i^u(\infty) < \mu_i^l$, (H3) implies that there is a unique $k_i > 0$ such that $B_i^u(k_i) - \mu_i^l = 0$. It follows from (H4) that there is an $N^0 > 0$ such that

$$(B_i^u(N) - \mu_i^l)N < - \sum_{j=1}^m k_j B_j^u(0+) - 1, \quad \forall N \geq N^0, \quad 1 \leq i \leq n.$$

Let $N^* = nN^0$. By the definition of N , it is easy to see that $N \geq N^*$ implies $N_{i_0} \geq N^0$ for some $1 \leq i_0 \leq n$. It then follows from (3.2.8) that

$$N'(t) \leq \sum_{j=1}^m B_j^u(0+)k_j + (B_{i_0}^u(N_{i_0}) - \mu_{i_0}^l)N_{i_0} < -1, \quad \text{if } N(t) \geq N^*,$$

which implies that G_N , $N \geq N^*$ is positively invariant and every forward orbit eventually enters into G_{N^*} . ■

Let $S^*(t)$ be the positive periodic solution of (3.2.6) with $S^*(0) = S^*$. Define

$$M_1(t) := \begin{bmatrix} \bar{b}_{11}(t) & \cdots & b_{1n}(t) \\ b_{21}(t) & \cdots & b_{2n}(t) \\ \vdots & \ddots & \vdots \\ b_{n1}(t) & \cdots & \bar{b}_{nn}(t) \end{bmatrix},$$

where $\bar{b}_{ii}(t) = \beta_i(t)S_i^*(t) - \mu_i(t) - \gamma_i(t) + b_{ii}(t)$, $1 \leq i \leq n$. Clearly, $M_1(t)$ is irreducible and has nonnegative off-diagonal elements.

In the case where the susceptible and infective individuals in each patch have the same dispersal rate, we have the following result on the global attractivity of the ω -periodic solution $(S^*(t), 0)$.

Theorem 3.2.3 *Let (H1)-(H5) hold and $r(\Phi_{M_1(\cdot)}(\omega)) < 1$. If $a_{ij}(t) = b_{ij}(t)$ for $1 \leq i, j \leq n$, $\forall t \in [0, \omega]$, then $\lim_{t \rightarrow \infty} (S(t) - S^*(t)) = 0$, $\lim_{t \rightarrow \infty} I(t) = 0$ for all $(S^0, I^0) \in (\mathbb{R}_+^n \setminus \{0\}) \times \mathbb{R}_+^n$.*

Proof. Let us consider a nonnegative solution $(S(t), I(t))$ of (3.1.3). We want to show that

$$\lim_{t \rightarrow \infty} I(t) = 0. \tag{3.2.9}$$

By (3.1.3), we have

$$N'_i = B_i(t, N_i)N_i - \mu_i(t)N_i + \sum_{j=1}^n a_{ij}(t)N_j, \quad 1 \leq i \leq n. \quad (3.2.10)$$

By the aforementioned conclusion for (3.2.6), the Poincaré map associated with (3.2.10) has a unique positive fixed point $S^*(0)$ which is globally attractive in $\mathbb{R}_+^n \setminus \{0\}$.

It then follows that for any $\epsilon > 0$, there holds $N(t) = S(t) + I(t) < S^*(t) + \bar{\epsilon}$, where $\bar{\epsilon} = (\epsilon, \dots, \epsilon) \in \text{Int}(\mathbb{R}_+^n)$, when t is sufficiently large. Thus, if t is sufficiently large, we have

$$I'_i < \beta_i(t)(S_i^*(t) + \epsilon)I_i - (\mu_i(t) + \gamma_i(t))I_i + \sum_{j=1}^n b_{ij}(t)I_j, \quad 1 \leq i \leq n. \quad (3.2.11)$$

It then suffices to show that positive solutions of the auxiliary system

$$\check{I}'_i = \beta_i(t)(S_i^*(t) + \epsilon)\check{I}_i - (\mu_i(t) + \gamma_i(t))\check{I}_i + \sum_{j=1}^n b_{ij}(t)\check{I}_j, \quad 1 \leq i \leq n, \quad (3.2.12)$$

tend to zero as t goes to infinity. Let $M_2(t)$ be the matrix defined by

$$M_2(t) := \text{diag}(\beta_1(t), \beta_2(t), \dots, \beta_n(t)).$$

Since $r(\Phi_{M_1(\cdot)}(\omega)) < 1$ and $r(\Phi_{M_1(\cdot) + \epsilon M_2(\cdot)}(\omega))$ is continuous for small ϵ , we can fix an $\epsilon > 0$ small enough such that $r(\Phi_{M_1(\cdot) + \epsilon M_2(\cdot)}(\omega)) < 1$. By Lemma 3.2.1, there is a positive, ω -periodic function $\bar{v}(t) = (\bar{v}_1(t), \bar{v}_2(t), \dots, \bar{v}_n(t))$ such that $\rho e^{\tilde{\mu}t} \bar{v}(t)$ is a solution of (3.2.12) for any constant ρ , where $\tilde{\mu} = \frac{1}{\omega} \ln r(\Phi_{M_1(\cdot) + \epsilon M_2(\cdot)}(\omega))$. $\forall I^0 \in \mathbb{R}_+^n$, We can choose a real number $\rho^0 > 0$ such that $I^0 \leq \rho^0 \bar{v}(0)$. By the standard comparison theorem (see, e.g., [43, Theorem A.4]), we then get (3.2.9).

For any $(S^0, I^0) \in (\mathbb{R}_+^n \setminus \{0\}) \times \mathbb{R}_+^n$, we have $N^0 = S^0 + I^0 \in \mathbb{R}_+^n \setminus \{0\}$. By the global attractivity of $S^*(0)$ for P_1 , it then follows that $\lim_{t \rightarrow \infty} (S(t) - S^*(t)) = \lim_{t \rightarrow \infty} (N(t) - I(t) - S^*(t)) = 0$. ■

If the susceptible and infective individuals in each patch have different dispersal rate, and the initial value I^0 is small, we still have the result on the attractivity of the ω -periodic solution $(S^*(t), 0)$.

Theorem 3.2.4 *Let (H1)-(H5) hold and $r(\Phi_{M_1(\cdot)}(\omega)) < 1$. Then there exists $\delta > 0$ such that for every $(S^0, I^0) \in G_{N^*}$ with $S^0 \neq 0$ and $I_i^0 < \delta$, $1 \leq i \leq n$, the solution $(S(t), I(t))$ of (3.1.3) satisfies $\lim_{t \rightarrow \infty} (S(t) - S^*(t)) = 0$, $\lim_{t \rightarrow \infty} I(t) = 0$.*

Proof. Let us consider an auxiliary system,

$$\tilde{S}'_i = B_i(t, \tilde{S}_i)\tilde{S}_i - \mu_i(t)\tilde{S}_i + (B_i(t, 0+) + \gamma_i(t))\epsilon + \sum_{j=1}^n a_{ij}(t)\tilde{S}_j, \quad 1 \leq i \leq n \quad (3.2.13)$$

where $\epsilon > 0$ is a small constant to be determined. By (H5) and the previous analysis of system (3.2.6), we can restrict ϵ small enough such that (3.2.13) admits a globally attractive and positive ω -periodic solution $S^*(t, \epsilon)$. Let $S^\epsilon(t, N^*)$ be the solution of (3.2.13) through (N^*, \dots, N^*) at $t = 0$. We choose an integer $n_1 > 0$ such that

$$S^\epsilon(t, N^*) < S^*(t, \epsilon) + \bar{\epsilon}, \quad \forall t \geq n_1\omega.$$

Define a matrix $M_1(t, \epsilon)$ by

$$\begin{bmatrix} \beta_1(t)S_1^*(t, \epsilon) - \mu_1(t) - \gamma_1(t) + b_{11}(t) & \cdots & b_{1n}(t) \\ b_{21}(t) & \cdots & b_{2n}(t) \\ \vdots & \ddots & \vdots \\ b_{n1}(t) & \cdots & \beta_n(t)S_n^*(t, \epsilon) - \mu_n(t) - \gamma_n(t) + b_{nn}(t) \end{bmatrix}.$$

Since $M_1(t, 0) = M_1(t)$ and $r(\Phi_{M_1(\cdot, \epsilon) + \epsilon M_2(\cdot)}(\omega))$ is continuous for small ϵ , we can now choose ϵ small enough such that $r(\Phi_{M_1(\cdot, \epsilon) + \epsilon M_2(\cdot)}(\omega)) < 1$. By Lemma 3.2.1, there is a positive ω -periodic function $v(t) = (v_1(t), \dots, v_n(t))$ such that $\check{I}(t) = e^{\mu_3 t} v(t)$ is a solution of $\check{I}' = (M_1(t, \epsilon) + \epsilon M_2(t))\check{I}$, where $\mu_3 = \frac{1}{\omega} \ln r(\Phi_{M_1(\cdot, \epsilon) + \epsilon M_2(\cdot)}(\omega))$. Choose $k > 0$ small enough such that $kv(t) < \bar{\epsilon}$ for all $t \in [0, \omega]$.

Now we define another auxiliary system,

$$\hat{I}'_i = \beta_i(t)N^*\hat{I}_i - (\mu_i(t) + \gamma_i(t))\hat{I}_i + \sum_{j=1}^n b_{ij}(t)\hat{I}_j, \quad 1 \leq i \leq n. \quad (3.2.14)$$

Let $\hat{I}(t, \delta)$ be the solution of (3.2.14) through $(\delta, \dots, \delta) \in \mathbb{R}^n$ at $t = 0$. We choose $\delta > 0$ small enough such that

$$\hat{I}(t, \delta) < ke^{\mu_3 t} v(t) \leq kv(t) < \bar{\epsilon}, \quad \forall t \in [0, n_1 \omega]. \quad (3.2.15)$$

Let $(S(t), I(t))$ be a nonnegative solution of (3.1.3) with $(S^0, I^0) \in G_{N^*}$, $S^0 \neq 0$ and $I_i^0 < \delta$, $1 \leq i \leq n$. It then follows that $S(t) \gg 0$, $\forall t > 0$. We further claim that $I(t) \leq ke^{\mu_3 t} v(t)$, $\forall t \geq 0$. Suppose not. By the comparison principle and (3.2.15), there

exists a $q, 1 \leq q \leq n$, and a $T_1 > n_1\omega$ such that

$$\begin{aligned} I(t) &\leq ke^{\mu_3 t} v(t), & \text{for } 0 \leq t \leq T_1, \\ I_q(T_1) &= k(e^{\mu_3 T_1} v(T_1))_q, \\ I_q(t) &> k(e^{\mu_3 T_1} v(T_1))_q, & \text{for } 0 < t - T_1 \ll 1. \end{aligned} \quad (3.2.16)$$

Note that for $0 \leq t \leq T_1$, we have

$$S'_i < B_i(t, S_i)S_i - \mu_i(t)S_i + (B_i(t, 0+) + \gamma_i(t))\epsilon + \sum_{j=1}^n a_{ij}(t)S_j, \quad 1 \leq i \leq n. \quad (3.2.17)$$

It follows from the comparison principle that $S(T_1) < S^*(T_1, \epsilon) + \bar{\epsilon}$. Then, for $0 \leq t - T_1 \ll 1$, we have $S(t) < S^*(t, \epsilon) + \bar{\epsilon}$, and hence

$$I'_i < \beta_i(t)(S_i^*(t, \epsilon) + \epsilon)I_i - (\mu_i(t) + \gamma_i(t))I_i + \sum_{j=1}^n b_{ij}(t)I_j, \quad 1 \leq i \leq n.$$

Since $I(T_1) \leq ke^{\mu_3 T_1} v(T_1)$, the comparison principle implies that

$$I(t) < ke^{\mu_3 t} v(t), \quad \text{for } 0 \leq t - T_1 \ll 1,$$

and hence,

$$I_q(t) < k(e^{\mu_3 t} v(t))_q, \quad \text{for } 0 < t - T_1 \ll 1,$$

which contradicts to (3.2.16). This proves the claim.

By the above claim, (3.2.17) holds for all $t \geq 0$. Thus, the comparison principle implies that $S(t) < S^*(t, \epsilon) + \bar{\epsilon}$, $\forall t \geq n_1\omega$. A similar argument shows that

$$I(t) < ke^{\mu_3 t} v(t), \quad \forall t > T_1.$$

Consequently, $I(t) \rightarrow 0$ as $t \rightarrow \infty$.

Since $P^m(x^0) = u(m\omega, x^0)$, $\forall x^0 \in \mathbb{R}_+^{2n}$, we have

$$P^m(S^0, I^0) = u(m\omega, (S^0, I^0)) = (S(m\omega), I(m\omega)), \forall (S^0, I^0) \in \mathbb{R}_+^n \times \mathbb{R}_+^n.$$

Given $(S^0, I^0) \in G_{N^*}$ with $S^0 \neq 0$ and $I_i^0 < \delta$, $1 \leq i \leq n$, it easily follows that $S(t) \in \text{Int}(\mathbb{R}_+^n)$, $\forall t > 0$. Let

$$\omega = \omega(S^0, I^0) := \{(S_*, I_*) : \exists \{m_k\} \rightarrow \infty \text{ such that } \lim_{k \rightarrow \infty} P^{m_k}(S^0, I^0) = (S_*, I_*)\}$$

be the omega limit set of (S^0, I^0) for P . Since $\lim_{t \rightarrow \infty} I(t) = 0$, there holds $\omega = \bar{\omega} \times \{0\}$.

We claim that $\bar{\omega} \neq \{0\}$. Assume that, by contradiction, $\bar{\omega} = \{0\}$. $\lim_{n \rightarrow \infty} P^n(S^0, I^0) = (0, 0)$, then $\lim_{t \rightarrow \infty} S(t) = 0$. By assumption (H5), we can choose a small $\eta > 0$ such that $r(\Phi_{M(\cdot, 0) - \eta E}(\omega)) > 1$, where $E = \text{diag}(1, \dots, 1)$. It follows that there exists a $\bar{t} > 0$ such that

$$B_i(t, N_i(t)) - \beta_i(t)I_i(t) \geq B_i(t, 0+) - \eta, \quad \forall t \geq \bar{t}, \quad 1 \leq i \leq n.$$

Thus, $S(t) = (S_1(t), \dots, S_n(t))$ satisfies

$$S'_i(t) > (B_i(t, 0+) - \eta)S_i - \mu_i(t)S_i + \sum_{j=1}^n a_{ij}(t)S_j, \quad \forall t \geq \bar{t}, \quad 1 \leq i \leq n. \quad (3.2.18)$$

Let $p(t) = (p_1(t), \dots, p_n(t))$ be the positive ω -periodic function for which $e^{\mu_4 t} p(t)$ is a solution of the linear system

$$\hat{S}'_i = (B_i(t, 0+) - \eta)\hat{S}_i - \mu_i(t)\hat{S}_i + \sum_{j=1}^n a_{ij}(t)\hat{S}_j, \quad 1 \leq i \leq n, \quad (3.2.19)$$

where $\mu_4 = \frac{1}{\omega} \ln(r(\Phi_{M(\cdot, 0) - \eta E}(\omega))) > 0$. Since $S(\bar{t}) \in \text{Int}(\mathbb{R}_+^n)$, we can choose a small number $\alpha > 0$ such that $S(\bar{t}) \geq \alpha p(0)$. Then the comparison theorem implies that

$$S(t) \geq \alpha e^{\mu_4(t-\bar{t})} p(t-\bar{t}) \geq \alpha e^{\mu_4(t-\bar{t})} \min_{t-\bar{t} \geq 0} p(t-\bar{t}), \quad \forall t \geq \bar{t},$$

and hence $\lim_{t \rightarrow \infty} S_i(t) = \infty$, $1 \leq i \leq n$, a contradiction. Note that for any $S^0 \in \mathbb{R}_+^n$, we have $u(t, (S^0, 0)) = (u_1(t, S^0), 0)$, $\forall t \geq 0$. It thus follows that

$$P^m(S^0, 0) = (P_1^m(S^0), 0), \forall S^0 \in \mathbb{R}_+^n, m \geq 0.$$

Since ω is an internal chain transitive set for P , and hence $\bar{\omega}$ is an internal chain-transitive set for P_1 . Let

$$W^s(S^*(0)) := \{S^0 : P_1^m(S^0) \rightarrow S^*(0), m \rightarrow \infty\}.$$

Since $\bar{\omega} \neq \{0\}$ and $S^*(0)$ is globally attractive for P_1 in $\mathbb{R}_+^n \setminus \{0\}$, we have $\bar{\omega} \cap W^s(S^*(0)) \neq \emptyset$. By Lemma 1.1.11, we get $\bar{\omega} = \{S^*(0)\}$, and hence $\omega = \{(S^*(0), 0)\}$. Thus, $\lim_{t \rightarrow \infty} (S(t) - S^*(t)) = 0$ and $\lim_{t \rightarrow \infty} I(t) = 0$. ■

The following result shows that $r(\Phi_{M_1(\cdot)}(\omega))$ is a threshold parameter for the extinction and the uniform persistence of the disease. When $r(\Phi_{M_1(\cdot)}(\omega)) > 1$, the model (3.1.3) admits at least one positive periodic solution, and the disease is uniformly persistent.

Theorem 3.2.5 *Let (H1)-(H5) hold and $r(\Phi_{M_1(\cdot)}(\omega)) > 1$. Then system (3.1.3) admits at least one positive periodic solution, and there is a positive constant ϵ such that for all $(S^0, I^0) \in \mathbb{R}_+^n \times \text{Int}(\mathbb{R}_+^n)$, the solution $(S(t), I(t))$ of (3.1.3) satisfies*

$$\liminf_{t \rightarrow \infty} I_i(t) \geq \epsilon, \quad 1 \leq i \leq n.$$

Proof. Define

$$X := \mathbb{R}_+^{2n}, \quad X_0 := \mathbb{R}_+^n \times \text{Int}(\mathbb{R}_+^n), \quad \partial X_0 := X \setminus X_0.$$

We first prove that P is uniformly persistent with respect to $(X_0, \partial X_0)$. By the form of (3.1.3), it is easy to see that both X and X_0 are positively invariant. Clearly, ∂X_0 is relatively closed in X . Furthermore, system (3.1.3) is point dissipative (see Lemma 3.2.2). Set

$$M_\partial = \{(S^0, I^0) \in \partial X_0 : P^m(S^0, I^0) \in \partial X_0, \forall m \geq 0\}.$$

We now show that

$$M_\partial = \{(S, 0) : S \geq 0\}. \quad (3.2.20)$$

Obviously, $\{(S, 0) : S \geq 0\} \subseteq M_\partial$.

For any $(S^0, I^0) \in \partial X_0 \setminus \{(S, 0) : S \geq 0\}$, we partition $\{1, 2, \dots, n\}$ into two sets Q_1 and Q_2 such that

$$I_j^0 = 0, \quad \forall j \in Q_1,$$

$$I_i^0 > 0, \quad \forall i \in Q_2,$$

where Q_1 and Q_2 are nonempty. For all $j \in Q_1, i \in Q_2$, we have

$$I_j'(0) \geq b_{ji}I_i(0) > 0.$$

It follows that $(S(t), I(t)) \notin \partial X_0$ for $0 < t \ll 1$. Thus, the positive invariance of X_0 implies (3.2.20). It is clear that there are two fixed points of P in M_∂ , which are $M_0 = (0, 0)$ and $M_1 = (S^*(0), 0)$.

Choose $\eta > 0$ small enough such that $r(\Phi_{M_1(\cdot) - \eta M_2(\cdot)}(\omega)) > 1$. Let us consider a perturbed system of (3.2.6)

$$\hat{S}_i' = B_i(t, \hat{S}_i + \delta)\hat{S}_i - (\mu_i(t) + \beta_i(t)\delta)\hat{S}_i + \sum_{j=1}^n a_{ij}(t)\hat{S}_j, \quad 1 \leq i \leq n. \quad (3.2.21)$$

As in our previous analysis of system (3.2.6), we can choose $\delta > 0$ small enough such that the Poincaré map associated with (3.2.21) admits a unique positive fixed point $S^*(0, \delta)$ which is globally attractive in $\mathbb{R}_+^n \setminus \{0\}$. By the Implicit Function Theorem, it follows that $S^*(0, \delta)$ is continuous in δ . Thus, we can fix a small number $\delta > 0$ such that $S^*(t, \delta) > S^*(t) - \bar{\eta}$, $\forall t \geq 0$, where $\bar{\eta} = (\eta, \dots, \eta)$. By the continuity of solutions with respect to the initial values, there exists $\delta_0^* > 0$ such that for all $(S^0, I^0) \in X_0$ with $\|(S^0, I^0) - M_i\| \leq \delta_0^*$, we have $\|u(t, (S^0, I^0)) - u(t, M_i)\| < \delta$, $\forall t \in [0, \omega]$, $i = 0, 1$. We now claim that

$$\limsup_{m \rightarrow \infty} d(P^m(S^0, I^0), M_i) \geq \delta_0^*, \quad i = 0, 1.$$

Suppose, by contradiction, that $\limsup_{n \rightarrow \infty} d(P^n(S^0, I^0), M_i) < \delta_0^*$ for some $(S^0, I^0) \in X_0$ and i . Without loss of generality, we can assume that $d(P^m(S^0, I^0), M_i) < \delta_0^*$, $\forall m \geq 0$. Then, we have $\|u(t, P^m(S^0, I^0)) - u(t, M_i)\| < \delta$, $\forall m \geq 0, \forall t \in [0, \omega]$. For any $t \geq 0$, let $t = m\omega + t'$, where $t' \in [0, \omega)$ and $m = [\frac{t}{\omega}]$ is the greatest integer less than or equal to $\frac{t}{\omega}$. Thus, we get

$$\|u(t, (S^0, I^0)) - u(t, M_i)\| = \|u(t', P^m(S^0, I^0)) - u(t', M_i)\| < \delta, \quad \forall t \geq 0.$$

Let $(S(t), I(t)) = u(t, (S^0, I^0))$. It then follows that $0 \leq I_i(t) \leq \delta$, $\forall t \geq 0, \forall 1 \leq i \leq n$.

Then for $t \geq 0$, we have

$$S'_i \geq B_i(t, S_i + \delta)S_i - (\mu_i(t) + \beta_i(t)\delta)S_i + \sum_{j=1}^n a_{ij}(t)S_j, \quad 1 \leq i \leq n. \quad (3.2.22)$$

Since the fixed point $S^*(0, \delta)$ of the Poincaré map associated with (3.2.21) is globally attractive and $S^*(t, \delta) > S^*(t) - \bar{\eta}$, there is a $T > 0$ such that $S(t) \geq S^*(t) - \bar{\eta}$ for

$t \geq T$. As a consequence, for $t \geq T$, there holds

$$I'_i \geq \beta_i(t)(S_i^*(t) - \eta)I_i - (\mu_i(t) + \gamma_i(t))I_i + \sum_{j=1}^n b_{ij}(t)I_j, \quad 1 \leq i \leq n. \quad (3.2.23)$$

Since $r(\Phi_{M_1(\cdot) - \eta M_2(\cdot)}(\omega)) > 1$, it is easy to see that $\lim_{t \rightarrow \infty} I_i(t) = \infty$, $i = 1, 2, \dots, n$, which leads to a contradiction.

Note that $S^*(0)$ is globally attractive in $\mathbb{R}_+^n \setminus \{0\}$ for P_1 . By the aforementioned claim, it follows that M_0 and M_1 are isolated invariant sets in X , $W^s(M_0) \cap X_0 = \emptyset$, and $W^s(M_1) \cap X_0 = \emptyset$. Clearly, every orbit in M_∂ converges to either M_0 or M_1 , and M_0 and M_1 are acyclic in M_∂ . By Theorem 1.1.4 for a stronger repelling property of ∂X_0 , we conclude that P is uniformly persistent with respect to $(X_0, \partial X_0)$. Thus, Theorem 1.1.3 implies the uniform persistence of the solutions of system (3.1.3) with respect to $(X_0, \partial X_0)$. By Theorem 1.1.5, P has a fixed point $(\bar{S}(0), \bar{I}(0)) \in X_0$. Then $\bar{S}(0) \in \mathbb{R}_+^n$ and $\bar{I}(0) \in \text{Int}(\mathbb{R}_+^n)$. We further claim that $\bar{S}(0) \in \mathbb{R}_+^n \setminus \{0\}$. Suppose that $\bar{S}(0) = 0$. By the second equation in (3.1.4), we obtain $0 = -\sum_{i=1}^n (\mu_i(t) + \gamma_i(t))\bar{I}_i(0)$, and hence $\bar{I}_i(0) = 0$, $i = 1, 2, \dots, n$, a contradiction. By the first equation in (3.1.3) and the irreducibility of the cooperative matrix $(a_{ij}(t))$, it follows that $u(t, (\bar{S}(0), \bar{I}(0))) \in \text{Int}(\mathbb{R}_+^n)$, $\forall t > 0$. Thus, $(\bar{S}(0), \bar{I}(0))$ is a componentwise positive fixed point of P . Thus, $(\bar{S}(t), \bar{I}(t))$ is a positive ω -periodic solution of (3.1.3). ■

3.3 The positive periodic solutions

In the case where the dispersal rates of susceptible individuals and infective individuals are equal, we are able to prove the uniqueness and global asymptotic stability of the positive ω -periodic solution under the condition that $r(\Phi_{M_1(\cdot)}(\omega)) > 1$.

Theorem 3.3.1 *Let (H1)-(H5) hold and $r(\Phi_{M_1(\cdot)}(\omega)) > 1$. If $a_{ij}(t) = b_{ij}(t)$ for $1 \leq i, j \leq n, \forall t \in [0, \omega]$, then the system (3.1.3) admits a unique positive ω -periodic solution which is globally asymptotically stable in $\mathbb{R}_+^n \times (\mathbb{R}_+^n \setminus \{0\})$.*

Proof. By (3.1.3), when $a_{ij}(t) = b_{ij}(t)$, we have

$$\begin{cases} S'_i = B_i(t, N_i)N_i - \mu_i(t)S_i - \beta_i(t)S_iI_i + \gamma_i(t)I_i + \sum_{j=1}^n a_{ij}(t)S_j, & 1 \leq i \leq n, \\ I'_i = \beta_i(t)S_iI_i - (\mu_i(t) + \gamma_i(t))I_i + \sum_{j=1}^n a_{ij}(t)I_j, & 1 \leq i \leq n. \end{cases} \quad (3.3.24)$$

Hence we obtain

$$N'_i = B_i(t, N_i)N_i - \mu_i(t)N_i + \sum_{j=1}^n a_{ij}(t)N_j, \quad 1 \leq i \leq n. \quad (3.3.25)$$

By the aforementioned conclusion for (3.2.6), the Poincaré map associated with (3.3.25) has a unique positive fixed point $S^*(0)$ which is globally attractive for $N \in \mathbb{R}_+^n \setminus \{0\}$. Thus (3.3.24) is equivalent to the following system:

$$\begin{cases} N'_i = B_i(t, N_i)N_i - \mu_i(t)N_i + \sum_{j=1}^n a_{ij}(t)N_j, & 1 \leq i \leq n, \\ I'_i = \beta_i(t)(N_i - I_i)I_i - (\mu_i(t) + \gamma_i(t))I_i + \sum_{j=1}^n a_{ij}(t)I_j, & 1 \leq i \leq n. \end{cases} \quad (3.3.26)$$

Since $\lim_{t \rightarrow \infty} (N(t) - S^*(t)) = 0$, the second equation of (3.3.26) has the following limiting system:

$$\tilde{I}'_i = \beta_i(t)(S_i^*(t) - \tilde{I}_i)\tilde{I}_i - (\mu_i(t) + \gamma_i(t))\tilde{I}_i + \sum_{j=1}^n a_{ij}(t)\tilde{I}_j, \quad 1 \leq i \leq n. \quad (3.3.27)$$

Let $F_1 : \mathbb{R}_+^1 \times \mathbb{R}_+^n \rightarrow \mathbb{R}^n$ be defined by the right-hand side of (3.3.27). Clearly, F_1 satisfies (M1) – (M4). Let $P_2 : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ be the Poincaré map associated with (3.3.27), that is,

$$P_2(I^0) = u_2(\omega, I^0), \quad \forall I^0 \in \mathbb{R}_+^n,$$

where $u_2(t, I^0)$ is the solution of (3.3.27) with $u_2(0, I^0) = I^0$. We claim that (3.3.27) admits a bounded positive solution.

Define

$$M_2(t, Z) := \begin{bmatrix} \bar{a}_{11}(t) & \cdots & a_{1n}(t) \\ a_{21}(t) & \cdots & a_{2n}(t) \\ \vdots & \ddots & \vdots \\ a_{n1}(t) & \cdots & \bar{a}_{nn}(t) \end{bmatrix},$$

where $\bar{a}_{ii}(t) = \beta_i(t)(S_i^*(t) - Z) - \mu_i(t) - \gamma_i(t) + a_{ii}(t)$, $1 \leq i \leq n$. We can choose a sufficiently large real number $Z > 0$ such that $\int_0^\omega (\beta_i(t)(S_i^*(t) - Z) - \mu_i(t) - \gamma_i(t))dt < 0$, $1 \leq i \leq n$. By Lemma 3.2.1, there is a positive, ω -periodic function $v(t) = (v_1(t), v_2(t), \dots, v_n(t))$ such that $V(t) = e^{\mu_5 t} v(t)$ is a solution of $V' = M_2(t, Z)V$, where $\mu_5 = \frac{1}{\omega} \ln r(\Phi_{M_2(\cdot, Z)}(\omega))$. Let $\Sigma(t) = \sum_{i=1}^n V_i(t) = e^{\mu_5 t} \sum_{i=1}^n v_i(t)$. By the first equation in (3.1.4), it easily follows that $\Sigma'(t) \leq b(t)\Sigma(t)$, $\forall t \geq 0$, where $b(t) = \max\{\beta_i(t)(S_i^*(t) - Z) - \mu_i(t) - \gamma_i(t) : 1 \leq i \leq n\}$. Thus, $\lim_{t \rightarrow \infty} \Sigma(t) = 0$, and hence

$\mu_5 < 0$, i.e., $r(\Phi_{M_2(\cdot, Z)}(\omega)) < 1$. Choose $l > 0$ large enough such that $lv_i(t) > Z$, $\forall t \in [0, \omega], i = 1, 2, \dots, n$. Set $H(t) \equiv lv(t)$. If we rewrite (3.3.27) as $\tilde{I}' = F_1(t, \tilde{I})$, it is easy to see that

$$F_1(t, H(t)) < M_2(t, Z)H(t), \quad \forall t \geq 0. \quad (3.3.28)$$

By the standard comparison theorem (see, e.g., [43, Theorem B.1]), it follows that

$$\begin{aligned} 0 < u_2(m\omega, lv(0)) &\leq \Phi_{M_2(\cdot, Z)}(m\omega)lv(0) = r(\Phi_{M_2(\cdot, Z)}(m\omega))lv(0) \\ &= r(\Phi_{M_2(\cdot, Z)}(\omega))^m lv(0) < lv(0), \quad \forall m \geq 0. \end{aligned}$$

That is, $P_2^m(lv(0)) < lv(0), \forall m \geq 0$. Consequently, $P_2^m(lv(0))$ is bounded. Since $r(\Phi_{M_2(\cdot, 0)}(\omega)) = r(\Phi_{M_1(\cdot)}(\omega)) > 1$. By [63, Theorem 2.1.2], it follows that the Poincaré map P_2 has a unique positive fixed point $\bar{I}(0)$ which is globally attractive for $I^0 \in \mathbb{R}_+^n \setminus \{0\}$. Thus, the Poincaré map P associated with (3.3.24) admits a unique fixed point $(S^*(0) - \bar{I}(0), \bar{I}(0))$. It then follows from Theorem 2.3 that the unique fixed point is positive. We denote it by $(\bar{S}(0), \bar{I}(0))$.

Let $P_3 : X := \mathbb{R}_+^{2n} \rightarrow \mathbb{R}_+^{2n}$ be the Poincaré map associated with (3.3.26), that is,

$$P_3(x^0) = u_3(\omega, x^0), \quad \forall x^0 \in \mathbb{R}_+^{2n},$$

where $u_3(t, x^0)$ is the solution of (3.3.26) with $u_3(0, x^0) = x^0$. Thus, we have

$$P_3^m(N^0, I^0) = u_3(m\omega, (N^0, I^0)), \quad \forall (N^0, I^0) \in \mathbb{R}_+^n \times \mathbb{R}_+^n.$$

Let $(N^0, I^0) \in (\mathbb{R}_+^n \setminus \{0\}) \times (\mathbb{R}_+^n \setminus \{0\})$ be fixed. It then follows that

$$(N(t), I(t)) = u_3(t, (N^0, I^0)) \in \text{Int}(\mathbb{R}_+^n) \times \text{Int}(\mathbb{R}_+^n), \quad \forall t > 0.$$

Let $\omega = \omega(N^0, I^0)$ be the omega limit set of (N^0, I^0) for P_3 . Since $\lim_{t \rightarrow \infty} (N(t) - S^*(t)) = 0$, there holds $\omega = \{S^*(0)\} \times \tilde{\omega}$. We claim that $\tilde{\omega} \neq \{0\}$. Assume that, by contradiction, $\tilde{\omega} = \{0\}$. Then $\lim_{m \rightarrow \infty} P_3^m(N^0, I^0) = (S^*(0), 0)$, that is, $\lim_{t \rightarrow \infty} (N(t) - S^*(t)) = 0$, $\lim_{t \rightarrow \infty} I(t) = 0$. Since $r(\Phi_{M_1(\cdot)}(\omega)) > 1$, we can choose a small $\eta > 0$ such that $r(\Phi_{M_1(\cdot) - \eta E}(\omega)) > 1$, where $E = \text{diag}(1, \dots, 1)$. It follows that there exists a $\bar{t} > 0$ such that

$$\beta_i(t)(N_i(t) - I_i(t)) \geq \beta_i(t)S_i^*(t) - \eta, \quad \forall t \geq \bar{t}, \quad 1 \leq i \leq n.$$

Thus $I(t) = (I_1(t), \dots, I_n(t))$ satisfies

$$I_i' > (\beta_i(t)S_i^*(t) - \eta)I_i - (\mu_i(t) + \gamma_i(t))I_i + \sum_{j=1}^n a_{ij}(t)I_j, \quad \forall t \geq \bar{t}, \quad 1 \leq i \leq n. \quad (3.3.29)$$

Let $q(t) = (q_1(t), \dots, q_n(t))$ be the positive ω -periodic function such that $e^{\mu_6 t} q(t)$ is a solution of the linear system

$$\hat{I}_i' = (\beta_i(t)S_i^*(t) - \eta)\hat{I}_i - (\mu_i(t) + \gamma_i(t))\hat{I}_i + \sum_{j=1}^n a_{ij}(t)\hat{I}_j, \quad 1 \leq i \leq n, \quad (3.3.30)$$

where $\mu_6 = \frac{1}{\omega} \ln(r(\Phi_{M_1(\cdot) - \eta E}(\omega))) > 0$. Since $I(\bar{t}) \in \text{Int}(\mathbb{R}_n^+)$, we can choose a small number $\alpha > 0$ such that $I(\bar{t}) \geq \alpha q(0)$. Then the comparison theorem implies that

$$I(t) \geq \alpha e^{\mu_6(t-\bar{t})} q(t - \bar{t}) \geq \alpha e^{\mu_6(t-\bar{t})} \min_{t-\bar{t} \geq 0} q(t - \bar{t}), \quad \forall t \geq \bar{t},$$

and hence $\lim_{t \rightarrow \infty} I_i(t) = \infty$, $1 \leq i \leq n$, a contradiction. Note that for any $I^0 \in \mathbb{R}_+^n$, we have $u_3(t, (S^*(0), I^0)) = (S^*(t), u_2(t, I^0))$, $\forall t \geq 0$. It then follows that

$$P_3^m(S^*(0), I^0) = (S^*(0), P_2^m(I^0)), \quad \forall I^0 \in \mathbb{R}_+^n, m \geq 0.$$

Since ω is an internal chain-transitive set for P_3 , $\tilde{\omega}$ is an internal chain transitive set for P_2 . Let

$$W^s(\bar{I}(0)) := \{I^0 : \lim_{m \rightarrow \infty} (P_2^m(I^0)) = \bar{I}(0)\}.$$

Since $\tilde{\omega} \neq \{0\}$ and $\bar{I}(0)$ is globally attractive for P_2 in $\mathbb{R}_+^n \setminus \{0\}$, we have $\tilde{\omega} \cap W^s(\bar{I}(0)) \neq \emptyset$. By Theorem 1.1.11, we then get $\tilde{\omega} = \{\bar{I}(0)\}$, and hence $\omega = \{(S^*(0), \bar{I}(0))\}$, which implies that the positive fixed point $(\bar{S}(0), \bar{I}(0))$ of P is globally attractive in $\mathbb{R}_+^n \times (\mathbb{R}_+^n \setminus \{0\})$. It follows that system (3.1.3) admits a unique positive ω -periodic solution $(\bar{S}(t), \bar{I}(t))$ such that $\lim_{t \rightarrow \infty} (S(t) - \bar{S}(t)) = 0$ and $\lim_{t \rightarrow \infty} (I(t) - \bar{I}(t)) = 0$, $\forall (S^0, I^0) \in \mathbb{R}_+^n \times (\mathbb{R}_+^n \setminus \{0\})$.

It remains to prove the stability of $(\bar{S}(t), \bar{I}(t))$ for (3.1.3), which is equivalent to the stability of $(\bar{N}(t), \bar{I}(t)) := (\bar{S}(t) + \bar{I}(t), \bar{I}(t))$ for (3.3.26). The associated Jacobian matrix is

$$A(t) = \begin{bmatrix} A_1(t) & 0 \\ A_2(t) & A_3(t) \end{bmatrix},$$

where

$$A_1(t) = \begin{bmatrix} a_{11}^*(t) & a_{12}(t) & \cdots & a_{1n}(t) \\ a_{21}(t) & a_{22}^*(t) & \cdots & b_{2n}(t) \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}(t) & a_{n2}(t) & \cdots & a_{nn}^*(t) \end{bmatrix}.$$

Here $a_{ii}^*(t) = \frac{\partial B_i(t, N_i)}{\partial N_i} \big|_{N_i = \bar{N}_i} \bar{N}_i + B_i(t, \bar{N}_i) - \mu_i(t) + a_{ii}(t)$,

$$A_2(t) = \text{diag}(\beta_1(t)\bar{I}_1, \beta_2(t)\bar{I}_2, \dots, \beta_n(t)\bar{I}_n),$$

and

$$A_3(t) = \begin{bmatrix} b_{11}^*(t) & a_{12}(t) & \cdots & a_{1n}(t) \\ a_{21}(t) & b_{22}^*(t) & \cdots & b_{2n}(t) \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}(t) & a_{n2}(t) & \cdots & b_{nn}^*(t) \end{bmatrix},$$

with $b_{ii}^*(t) = \beta_i(t)\bar{N}_i - 2\beta_i(t)\bar{I}_i - \mu_i(t) - \gamma_i(t) + a_{ii}(t)$.

Obviously,

$$A_1(t) < \begin{bmatrix} \bar{a}_{11}^*(t) & a_{12}(t) & \cdots & a_{1n}(t) \\ a_{21}(t) & \bar{a}_{22}^*(t) & \cdots & b_{2n}(t) \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}(t) & a_{n2}(t) & \cdots & \bar{a}_{nn}^*(t) \end{bmatrix} := C_1(t),$$

with $\bar{a}_{ii}^*(t) = B_i(t, \bar{N}_i) - \mu_i(t) + a_{ii}(t)$, and

$$A_3(t) < \begin{bmatrix} \bar{b}_{11}^*(t) & a_{12}(t) & \cdots & a_{1n}(t) \\ a_{21}(t) & \bar{b}_{22}^*(t) & \cdots & b_{2n}(t) \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}(t) & a_{n2}(t) & \cdots & \bar{b}_{nn}^*(t) \end{bmatrix} := C_3(t),$$

with $\bar{b}_{ii}^*(t) = \beta_i(t)\bar{N}_i - \beta_i(t)\bar{I}_i - \mu_i(t) - \gamma_i(t) + a_{ii}(t)$. The comparison principle implies that $\Phi_{A_1(\cdot)}(t) \leq \Phi_{C_1(\cdot)}(t)$, $\Phi_{A_3(\cdot)}(t) \leq \Phi_{C_3(\cdot)}(t)$, and hence $\Phi_{A_1(\cdot)}(\omega) \leq \Phi_{C_1(\cdot)}(\omega)$, $\Phi_{A_3(\cdot)}(\omega) \leq \Phi_{C_3(\cdot)}(\omega)$. By [43, Theorem A.4], we have $\mu(\Phi_{A_1(\cdot)}(\omega)) < \mu(\Phi_{C_1(\cdot)}(\omega))$ and

$\mu(\Phi_{A_3(\cdot)}(\omega)) < \mu(\Phi_{C_3(\cdot)}(\omega))$. Notice that $(\bar{N}_1(t), \dots, \bar{N}_n(t))$ is a positive ω -periodic solution of the system $N' = C_1(t)N$. Thus, we have

$$\Phi_{C_1(\cdot)}(t) \begin{pmatrix} \bar{N}_1(0) \\ \vdots \\ \bar{N}_n(0) \end{pmatrix} = \begin{pmatrix} \bar{N}_1(t) \\ \vdots \\ \bar{N}_n(t) \end{pmatrix}.$$

It follows that

$$\Phi_{C_1(\cdot)}(\omega) \begin{pmatrix} \bar{N}_1(0) \\ \vdots \\ \bar{N}_n(0) \end{pmatrix} = \begin{pmatrix} \bar{N}_1(\omega) \\ \vdots \\ \bar{N}_n(\omega) \end{pmatrix} = \begin{pmatrix} \bar{N}_1(0) \\ \vdots \\ \bar{N}_n(0) \end{pmatrix},$$

and hence $\mu(\Phi_{C_1(\cdot)}(\omega)) = 1$. On the other hand, $(\bar{I}_1(t), \dots, \bar{I}_n(t))$ is a positive ω -periodic solution of the system $I' = C_3(t)I$. Thus, we obtain

$$\Phi_{C_3(\cdot)}(t) \begin{pmatrix} \bar{I}_1(0) \\ \vdots \\ \bar{I}_n(0) \end{pmatrix} = \begin{pmatrix} \bar{I}_1(t) \\ \vdots \\ \bar{I}_n(t) \end{pmatrix}.$$

It follows that

$$\Phi_{C_3(\cdot)}(\omega) \begin{pmatrix} \bar{I}_1(0) \\ \vdots \\ \bar{I}_n(0) \end{pmatrix} = \begin{pmatrix} \bar{I}_1(\omega) \\ \vdots \\ \bar{I}_n(\omega) \end{pmatrix} = \begin{pmatrix} \bar{I}_1(0) \\ \vdots \\ \bar{I}_n(0) \end{pmatrix},$$

and hence $\mu(\Phi_{C_3(\cdot)}(\omega)) = 1$. Consequently, we have

$$\mu(\Phi_A(\cdot)(\omega)) = \max\{\mu(\Phi_{A_1(\cdot)}(\omega)), \mu(\Phi_{A_3(\cdot)}(\omega))\} < 1,$$

which implies the stability of $(\bar{N}(t), \bar{I}(t))$. \blacksquare

At last, we prove the global attractivity of positive periodic solution in the case where $\{b_{ij}(t)\}$ is very close to $\{a_{ij}(t)\}$. Let Λ_0 be the set of all continuous and ω -periodic $n \times n$ matrix functions satisfying $a_{ij}(t) > 0, i \neq j, a_{ii}(t) < 0$ and $\sum_{j=1}^n a_{ji}(t) = 0$.

Theorem 3.3.2 *Assume (H1)-(H5) hold, Let $\lambda_0 = \{a_{ij}(t), 1 \leq i, j \leq n\} \in \Lambda_0$ be fixed, $\lambda = \{b_{ij}(t), 1 \leq i, j \leq n\} \in \Lambda_0$, $M_{1\lambda}(t)$ be the matrix $M_1(t)$ with parameter λ , and $M_{1\lambda_0}(t)$ be the matrix $M_{1\lambda}(t)$ with $\lambda = \lambda_0$. If $r(\Phi_{M_{1\lambda_0}(\cdot)}(\omega)) > 1$, then there exists $\epsilon > 0$ such that for any λ with $\|\lambda - \lambda_0\| \leq \epsilon$, the system (3.1.3) admits a unique positive ω -periodic solution $(\bar{S}_{\lambda_1}(t), \bar{S}_{\lambda_2}(t), \dots, \bar{S}_{\lambda_n}(t), \bar{I}_{\lambda_1}(t), \dots, \bar{I}_{\lambda_n}(t))$ such that $\lim_{t \rightarrow \infty} (S_i(t) - \bar{S}_{\lambda_i}(t)) = 0$ and $\lim_{t \rightarrow \infty} (I_i(t) - \bar{I}_{\lambda_i}(t)) = 0$ for every $(S^0, I^0) \in \mathbb{R}_+^n \times \text{Int}(\mathbb{R}_+^n)$.*

Proof. There exist $\epsilon_0 > 0, \eta > 0$, such that $r(\Phi_{M_{1\lambda}(\cdot)}(\omega)) > 1$ and $r(\Phi_{M_{1\lambda-\eta M_2}(\cdot)}(\omega)) > 1$ whenever $\|\lambda - \lambda_0\| \leq \epsilon_0$. We fix a sufficiently small $\delta > 0$ such that the Poincaré map associated with (3.2.21) admits a unique positive fixed point $S^*(0, \delta)$, which is globally attractive in $\mathbb{R}_+^n \setminus \{0\}$ and $S^*(t, \delta) > S^*(t) - \bar{\eta}$. Let $u(t, (S^0, I^0), \lambda)$ be the solution of (3.1.3) with parameter λ and initial value $(S^0, I^0) \in X$. By the continuity of solutions with respect to initial values and parameter λ , there exist positive numbers δ_0^* and ϵ_0^* such that $\|u(t, (S^0, I^0), \lambda) - u(t, M_i, \lambda_0)\| < \delta, \forall t \in [0, \omega]$, $\|(S^0, I^0) - M_i\| \leq \delta_0^*$ and $\|\lambda - \lambda_0\| \leq \epsilon_0^*, i = 0, 1$. Let $\epsilon^* = \min\{\epsilon_0, \epsilon_0^*\}$. By the argument similar to that of the claim in the proof of Theorem 3.2.3, it follows that

for any λ with $\|\lambda - \lambda_0\| \leq \epsilon^*$, and all $(S^0, I^0) \in \mathbb{R}_+^n \times \text{Int}(\mathbb{R}_+^n)$, there holds

$$\limsup_{m \rightarrow \infty} d(P_\lambda^m(S^0, I^0), M_i) \geq \delta_0^*, \quad i = 0, 1,$$

where P_λ is the Poincaré map associated with (3.1.3) with parameter λ . Moreover, Lemma 3.2.2 implies that solutions of (3.1.3) in X are uniformly bounded and ultimately bounded for each $\lambda \in \Lambda_0$. It follows that P has a global attractor $A_\lambda \subset X_0$ for each $\lambda \in \Lambda_0$. Let $\Lambda_1 = \Lambda_0 \cap \overline{\{\lambda : \|\lambda - \lambda_0\| \leq \epsilon^*\}}$. Then there exists a bounded and closed set G^* in $\mathbb{R}_+^n \times \mathbb{R}_+^n$, such that $\cup_{\lambda \in \Lambda_1} A_\lambda \subset G^*$. Hence, by Theorem 1.1.9, there exists a $\delta_0 > 0$ such that for any $\lambda \in \Lambda_1$,

$$\liminf_{m \rightarrow \infty} d(P_\lambda^m(S^0, I^0), \partial X_0) \geq \delta_0.$$

Since $\overline{\cup_{\lambda \in \Lambda_1} P(A_\lambda)} = \overline{\cup_{\lambda \in \Lambda_1} A_\lambda} \subset \overline{G^*} = G^*$, the set $\overline{\cup_{\lambda \in \Lambda_1} P(A_\lambda)}$ is compact. By applying Theorem 1.1.8 on the perturbation of a globally stable fixed point, we complete the proof. ■

3.4 Numerical simulations

In order to simulate the periodic solutions, we consider the case that the patch number is 2. For simplicity, we assume that the contact rate $\beta_i(t), i = 1, 2$, is ω -periodic with the expression $\beta_1(t) = \beta_2(t) = m \sin(pt) + q$, and other parameters are independent of time t . Then $\omega = \frac{2\pi}{p}$, and the assumption (3.1.4) is equivalent to that $a_{12} = -a_{22}$,

$a_{21} = -a_{11}$, $b_{12} = -b_{22}$, $b_{21} = -b_{11}$. Thus, (3.1.3) reduces to

$$\begin{cases} S'_1 = B_1(N_1)N_1 - (\mu_1 - a_{11})S_1 - \beta(t)S_1I_1 + \gamma_1I_1 - a_{22}S_2, \\ S'_2 = B_2(N_2)N_2 - (\mu_2 - a_{22})S_2 - \beta(t)S_2I_2 + \gamma_2I_2 - a_{11}S_1, \\ I'_1 = \beta(t)S_1I_1 - (\mu_1 + \gamma_1 - b_{11})I_1 - b_{22}I_2, \\ I'_2 = \beta(t)S_2I_2 - (\mu_2 + \gamma_2 - b_{22})I_2 - b_{11}I_1. \end{cases} \quad (3.4.31)$$

As mentioned in [4], we choose $B_i(N_i) = \frac{r_i}{N_i} + c_i$, where $c_i < \mu_i$, $i = 1, 2$. Suppose that

$$r_1 = r_2 = r, \quad c_1 = c_2 = c, \quad \mu_1 = \mu_2 = \mu, \quad \gamma_1 = \gamma_2 = \gamma, \quad a_{11} = a_{22} = b_{11} = b_{22} = -\theta < 0.$$

Then (3.4.31) reduces to

$$\begin{cases} S'_1 = r - (\mu + \theta - c)S_1 - (m \sin(pt) + q)S_1I_1 + (c + \gamma)I_1 + \theta S_2, \\ S'_2 = r - (\mu + \theta - c)S_2 - (m \sin(pt) + q)S_2I_2 + (c + \gamma)I_2 + \theta S_1, \\ I'_1 = (m \sin(pt) + q)S_1I_1 - (\mu + \gamma + \theta)I_1 + \theta I_2, \\ I'_2 = (m \sin(pt) + q)S_2I_2 - (\mu + \gamma + \theta)I_2 + \theta I_1. \end{cases} \quad (3.4.32)$$

It is easy to verify that conditions (H1)-(H5) are satisfied. In this case, $(S_1^*(t), S_2^*(t))$ can be obtained explicitly as

$$S_1^*(t) = S_2^*(t) = \frac{r}{\mu - c}, \quad \forall t \geq 0.$$

Under all assumptions above, we get

$$\begin{aligned} M_1(t) &= \begin{bmatrix} \beta(t)\frac{r}{\mu-c} - \mu - \gamma - \theta & \theta \\ \theta & \beta(t)\frac{r}{\mu-c} - \mu - \gamma - \theta \end{bmatrix} \\ &= \begin{bmatrix} -\mu - \gamma - \theta & \theta \\ \theta & -\mu - \gamma - \theta \end{bmatrix} + \begin{bmatrix} \beta(t)\frac{r}{\mu-c} & 0 \\ 0 & \beta(t)\frac{r}{\mu-c} \end{bmatrix}. \end{aligned}$$

Let A be a 2×2 constant matrix, and $\alpha(t)$ be a continuous ω -periodic function.

Note that if $x(t)$ is a solution of $x' = (A + \alpha(t)I)x$, then $y(t) = e^{\int_0^t -\alpha(s)ds} x(t)$ satisfies

$$\begin{aligned} y'(t) &= e^{\int_0^t -\alpha(s)ds} (x' - \alpha(t)x) \\ &= e^{\int_0^t -\alpha(s)ds} Ax(t) \\ &= Ae^{\int_0^t -\alpha(s)ds} x(t) \\ &= Ay(t) \end{aligned}$$

Thus, we have $\phi_{A+\alpha(\cdot)I}(t) = e^{\int_0^t \alpha(s)ds} e^{At}$.

By the above observation, it follows that $r(\Phi_{M_1(\cdot)}(\omega)) = e^{\frac{r}{\mu-c} \int_0^\omega \beta(t)dt} e^{-(\mu+\gamma)\omega}$. Fix $\mu = 0.2, c = 0.1, \theta = 1, \gamma = 4, m = 1, p = 2\pi, q = 0.1, r = 1$. Since $\omega = 1$, we have

$$r(\Phi_{M_1(\cdot)}(1)) < 1.$$

By Theorem 2.1, system (3.1.3) has a positive ω -periodic solution such that $\lim_{t \rightarrow \infty} (S(t) - S^*(t)) = 0$ and $\lim_{t \rightarrow \infty} I(t) = 0$ for all $(S^0, I^0) \in \mathbb{R}_+^n \times \mathbb{R}_+^n$. Our numerical simulations in Figure 3.1 confirm this result.

Fix $\mu = 2, c = 1, \theta = 1, \gamma = 0.1, m = 1, p = 2\pi, q = 1, r = 10$. We then have $\omega = 1$ and $r(\Phi_{M_1(\cdot)}(1)) > 1$. By Theorem 3.1, system (3.1.3) has a unique positive

ω -periodic solution such that $\lim_{t \rightarrow \infty} (S(t) - \bar{S}(t)) = 0$ and $\lim_{t \rightarrow \infty} (I(t) - \bar{I}(t)) = 0$ for all $(S^0, I^0) \in \mathbb{R}_+^n \times (\mathbb{R}_+^n \setminus \{0\})$. Our numerical simulations in Figure 3.2 confirm this result.

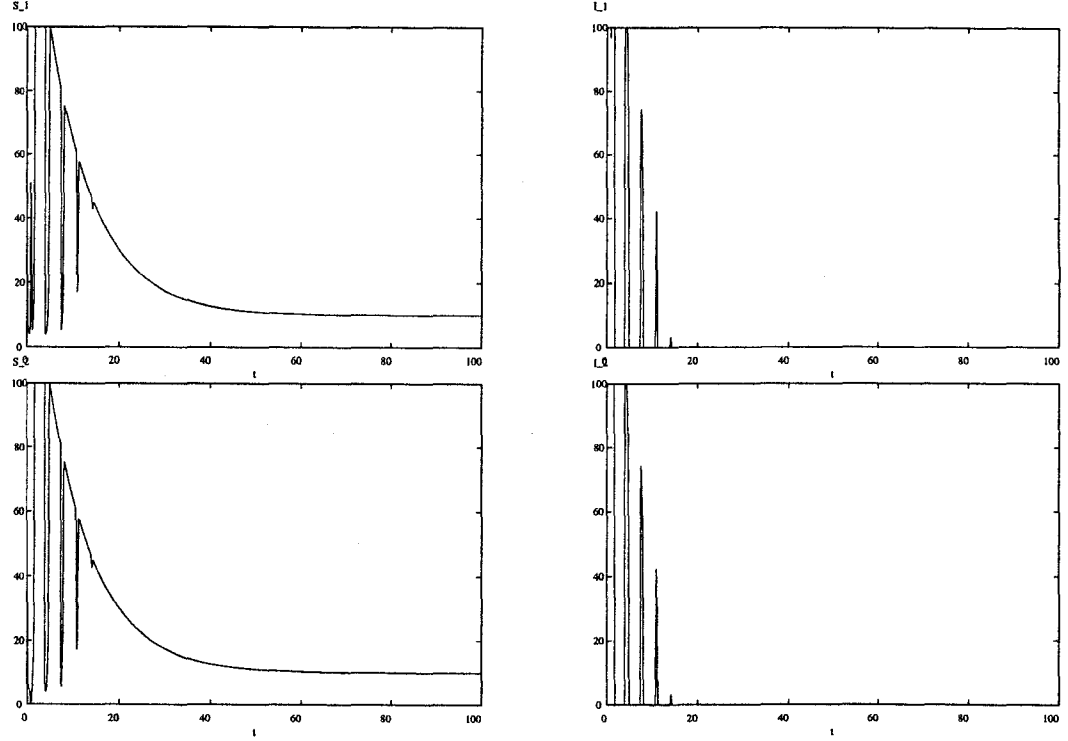


Figure 3.1: The solution of system (3.4.32): The extinction of the disease. The parameters of the system are as follows: $\mu = 0.2, c = 0.1, \theta = 1, \gamma = 4, m = 1, p = 2\pi, q = 0.1, r = 1$

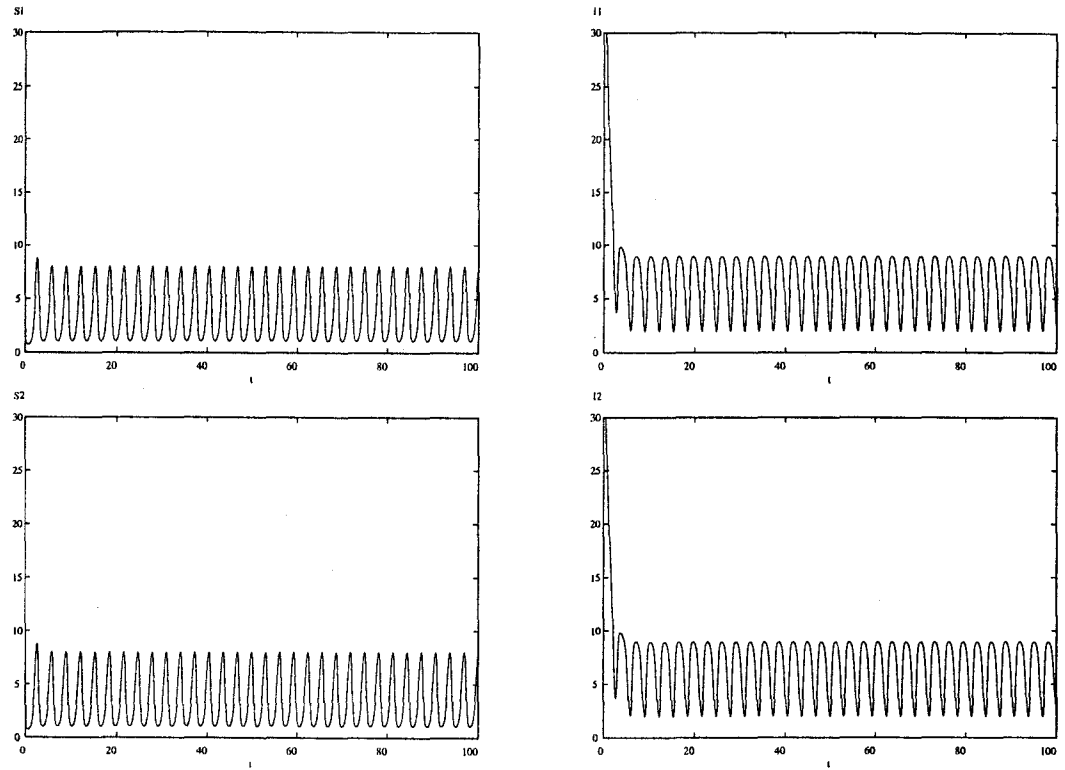


Figure 3.2: The solution of system (3.4.32): The uniform persistence

of the disease. The parameters of the system are as follows:

$$\mu = 2, c = 1, \theta = 1, \gamma = 0.1, m = 1, p = 2\pi, q = 1, r = 10$$

Chapter 4

A Lattice Epidemic Model

This chapter is devoted to the study of the asymptotic speed of spread and traveling waves for a spatially discrete SIS epidemic model. By appealing to the theory of spreading speeds and traveling waves for monotone semiflows, we establish the existence of asymptotic speed of spread and show that it coincides with the minimal wave speed for monotone traveling waves. This also gives an affirmative answer to an open problem presented by Rass and Radcliffe [41] in the case of a discrete spatial habitat.

This chapter is organized as follows. In Section 4.1, we present the model. The existence and comparison theorems for the single population system are established in Section 4.2. In Section 4.3, we prove the existence of an asymptotic spreading speed and show that it coincides with the minimal wave speed for monotone traveling waves. At last, we extend these results to the case of multi-populations in Section 4.4.

4.1 Introduction

The geographic spread of epidemics is an important subject in mathematical epidemiology (see, e.g., [12, 40, 41]). In order to consider the spreading speed of a deterministic epidemic in multi-type of populations, Rass and Radcliffe [41] presented the spatial epidemic model

$$\begin{aligned} \frac{dy_{j,m}(t)}{dt} &= (1 - y_{j,m}(t)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \sigma_m \lambda_{mn} y_{j-k,n}(t) p_{mn}(k) - \mu_m y_{j,m}(t), \\ j &\in \mathbb{Z}, \quad 1 \leq m \leq r, \end{aligned} \quad (4.1.1)$$

where $y_{j,m}(t)$ is the proportion of individuals in the m th population σ_m at position j who are infectious at time t , $\mu_m \geq 0$ is the combined death/emigration/recovery rate for infectious individuals, λ_{mn} is the infection rate of a type m susceptible by a type n infectious individual, and p_{mn} is the corresponding contact distribution. It is reasonable to assume that $\sum_{k=-\infty}^{\infty} p_{mn}(k) = 1$, and $p_{mn}(k) = p_{mn}(-k) \geq 0, \forall k \in \mathbb{Z}, 1 \leq m, n \leq r$. Since an epidemic often starts with a small amount of infection in a bounded region amongst the r types of populations at time $t = 0$, each $y_{j,m}(0)$ is assumed to have compact support. This model describes a closed system with no births, deaths, emigration or immigration, or an open system in which the birth and immigration rates are balanced by the death and emigration rates. The global dynamics of the spatially homogeneous r -dimensional system associated with (4.1.1) was analyzed completely in [41, Chapter 8]. However, as mentioned in [41, Section 8.8], there are no exact results for the asymptotic speed of propagation of infection

and traveling waves for models such as (4.1.1) in \mathbb{R}^n or \mathbb{Z}^n . This problem has been addressed recently by Weng and Zhao [56] for a spatially continuous version of model (4.1.1). Although there have been many investigations on traveling wave solutions and long-term behavior for lattice differential equations (see, e.g., [7, 36, 53, 55, 65] and references therein), the analysis of lattice differential systems with global interactions seems to be relatively difficult. Our purpose is to study the spreading speed and traveling waves for the lattice system (4.1.1) in the case where the spatial habitat is the integer lattice \mathbb{Z} , by appealing to the theory of spreading speeds and traveling waves for monotone semiflows, which was developed by Liang and Zhao [34] (see Section 1.3).

4.2 Existence and comparison of solutions

Let $(\mathbb{R}^k, \mathbb{R}_+^k)$ be the standard ordered k -dimensional Euclidean space with the maximum norm $\|\cdot\|$. For $\varsigma = (\varsigma_1, \dots, \varsigma_k), \xi = (\xi_1, \dots, \xi_k) \in \mathbb{R}^k$, we write $\varsigma \geq \xi$ ($\varsigma \gg \xi$) provided $\varsigma_i \geq \xi_i$ ($\varsigma_i > \xi_i$), $i = 1, \dots, k$, and $\varsigma > \xi$ provided $\varsigma \geq \xi$ but $\varsigma \neq \xi$. Let \mathbb{C} be the set of all bounded two-sided sequences of points in \mathbb{R}^k . For $u = (u_j)_{j \in \mathbb{Z}}, v = (v_j)_{j \in \mathbb{Z}} \in \mathbb{C}$, we write $u \geq v$ ($u \gg v$) provided $u_j \geq v_j$ ($u_j > v_j$), $\forall j \in \mathbb{Z}$, and $u > v$ provided $u \geq v$ but $u \neq v$. We regard any vector in \mathbb{R}^k as a constant sequence of points in \mathbb{R}^k , and set

$$\mathbb{R}_r^k := \{u \in \mathbb{R}^k : r \geq u \geq 0\}, \mathbb{C}_r := \{u \in \mathbb{C} : r \geq u \geq 0\},$$

for any $r \in \mathbb{R}^k$. We equip \mathbb{C} with the compact open topology, that is, $u^n \rightarrow u$ in \mathbb{C} means that the sequence of u_j^n converges to u_j as $n \rightarrow \infty$ uniformly for j in any bounded subset of \mathbb{Z} . Moreover, we define the metric function $d(\cdot, \cdot)$ in \mathbb{C} with respect to this topology by

$$d(u, v) := \sum_{k=0}^{\infty} \frac{\max_{|j| \leq k} \|u_j - v_j\|}{2^k}, \quad \forall u, v \in \mathbb{C},$$

so that (\mathbb{C}, d) is a metric space.

In order to study the asymptotic speed of spread and traveling waves of system (4.1.1), we first consider the following single population case:

$$\frac{dy_j(t)}{dt} = (1 - y_j(t))\sigma\lambda \sum_{k=-\infty}^{\infty} y_{j-k}(t)p(k) - \mu y_j(t), \quad j \in \mathbb{Z}, \quad (4.2.2)$$

where $y_j(t)$ is the proportion of infectious individuals at position j in the whole population σ at time t , $p(k)$ is the contact distribution with $\sum_{k=-\infty}^{\infty} p(k) = 1$. By the biological background, we assume that $p(k) = p(-k) \geq 0, \forall k \in \mathbb{Z}$. In this section, we establish the existence and uniqueness of the solutions, and the comparison theorem.

Theorem 4.2.1 *For any $y^0 \in \mathbb{C}_1$, (4.2.2) has a unique continuous solution $y(t, y^0)$ on $[0, \infty)$ such that $y(0, y^0) = y^0$ and $y(t, y^0) \in \mathbb{C}_1, \forall t \geq 0$.*

Proof. We first choose a sufficiently large number $D \geq \sigma\lambda$ such that

$$F_j(y) = Dy_j + (1 - y_j)\sigma\lambda \sum_{k=-\infty}^{\infty} y_{j-k}p(k), \quad \forall j \in \mathbb{Z},$$

is a monotone increasing mapping from \mathbb{C}_1 to \mathbb{R} . Clearly, (4.2.2) can be written as

$$\frac{dy_j(t)}{dt} = F_j(y) - (\mu + D)y_j(t), \quad (4.2.3)$$

The initial value problem of (4.2.3) is equivalent to

$$\begin{cases} y_j(t) = e^{-(\mu+D)t}y_j(0) + \int_0^t e^{-(\mu+D)(t-s)}F_j(y)ds, \quad \forall j \in \mathbb{Z}, \\ y(0) = y^0. \end{cases} \quad (4.2.4)$$

For any $y^0 \in \mathbb{C}_1$, and any $T \in (0, \infty)$, define

$$S_T =: \{y = \{y_j\}_{j \in \mathbb{Z}} : y_j \in C([0, T], [0, 1]), y(0) = y^0, \forall j \in \mathbb{Z}\},$$

and an operator $H^T = \{H_j^T\}_{j \in \mathbb{Z}}$ on S_T by

$$H_j^T(y)(t) = e^{-(\mu+D)t}y_j^0 + \int_0^t e^{-(\mu+D)(t-s)}F_j(y)ds, \forall y \in S_T, \forall j \in \mathbb{Z}.$$

Since

$$\begin{aligned} 0 &\leq H_j^T(y)(t) \leq e^{-(\mu+D)t} + F_j(1) \int_0^t e^{-(\mu+D)(t-s)}ds \\ &= \frac{D}{\mu+D} + e^{-(\mu+D)t} \frac{\mu}{\mu+D} \leq 1, \quad \forall t \in [0, T], \end{aligned}$$

we have $H^T(S_T) \subseteq S_T$. For any $\beta > 0$, we define

$$\|y\|_\beta := \sup_{t \in [0, T], j \in \mathbb{Z}} |y_j(t)|e^{-\beta t}, \forall y \in S_T.$$

Then $(S_T, \|\cdot\|)$ is a Banach space. For any $y, \bar{y} \in S_T$, let $w = \{w_j\}_{j \in \mathbb{Z}}$ with $w_j = \bar{y}_j - y_j$.

We then have

$$\begin{aligned}
& H_j^T(\bar{y})(t) - H_j^T(y)(t) \\
&= \int_0^t e^{-(\mu+D)(t-s)} (F_j(\bar{y}(s)) - F_j(y(s))) ds \\
&= \int_0^t e^{-(\mu+D)(t-s)} [Dw_j(s) + (1 - \bar{y}_j(s))\sigma\lambda \sum_{k=-\infty}^{\infty} \bar{y}_{j-k}(s)p(k) - (1 - y_j(s)) \\
&\quad \sigma\lambda \sum_{k=-\infty}^{\infty} y_{j-k}(s)p(k)] ds \\
&= \int_0^t e^{-(\mu+D)(t-s)} [Dw_j(s) + \sigma\lambda \sum_{k=-\infty}^{\infty} w_{j-k}(s)p(k) + \sigma\lambda \sum_{k=-\infty}^{\infty} (y_j(s)y_{j-k}(s) \\
&\quad - \bar{y}_j(s)\bar{y}_{j-k}(s))p(k)] ds \\
&= \int_0^t e^{-(\mu+D)(t-s)} [Dw_j(s) + \sigma\lambda \sum_{k=-\infty}^{\infty} w_{j-k}(s)p(k) + \sigma\lambda \sum_{k=-\infty}^{\infty} (\bar{y}_{j-k}(s)w_j(s) \\
&\quad - y_j(s)w_{j-k}(s))p(k)] ds,
\end{aligned}$$

which leads to

$$\begin{aligned}
& |H_j^T(\bar{y})(t) - H_j^T(y)(t)|e^{-\beta t} \\
&\leq \int_0^t e^{-\beta(t-s)-\beta s} [D|w_j(s)| + \sigma\lambda \sum_{k=-\infty}^{\infty} |w_{j-k}(s)|p(k) + \sigma\lambda \sum_{k=-\infty}^{\infty} (\bar{y}_{j-k}(s)|w_j(s)| \\
&\quad - y_j(s)|w_{j-k}(s)|)p(k)] ds \\
&\leq \int_0^t e^{-\beta(t-s)-\beta s} [D|w_j(s)| + 2\sigma\lambda \sum_{k=-\infty}^{\infty} |w_{j-k}(s)|p(k) + \sigma\lambda \sum_{k=-\infty}^{\infty} |w_j(s)|p(k)] ds.
\end{aligned}$$

Thus, we have

$$\begin{aligned}
\|H^T(\bar{y}) - H^T(y)\|_{\beta} &= \sup_{t \in [0, T], j \in \mathbb{Z}} |H_j^T(\bar{y})(t) - H_j^T(y)(t)|e^{-\beta t} \\
&\leq \frac{3\sigma\lambda + D}{\beta} (1 - e^{-\beta T}) \|w\|_{\beta} \\
&= \frac{3\sigma\lambda + D}{\beta} (1 - e^{-\beta T}) \|\bar{y} - y\|_{\beta}.
\end{aligned}$$

Since

$$\lim_{\beta \rightarrow \infty} \frac{3\sigma\lambda + D}{\beta} (1 - e^{-\beta T}) = 0, \quad (4.2.5)$$

it follows that for sufficiently large β , H^T is a contraction map on S_T , and hence, H^T has a unique fixed point y in S_T . This shows that (4.2.2) has a unique solution on $[0, T]$, $\forall T \in (0, \infty)$, which implies the existence and uniqueness of a solution $y(t)$ of (4.2.2) on $[0, \infty)$. ■

In order to establish the comparison theorem for system (4.2.2), we introduce the following concept of upper and lower solutions.

Definition 4.2.1 A function $y(t) = (y_j(t))_{j \in \mathbb{Z}}$ with $y_j \in C^1([0, \infty), [0, 1])$ is called an upper solution of (4.2.2) if it satisfies

$$\frac{dy_j(t)}{dt} \geq (1 - y_j(t))\sigma\lambda \sum_{k=-\infty}^{\infty} y_{j-k}(t)p(k) - \mu y_j(t), \quad \forall t \geq 0, j \in \mathbb{Z}. \quad (4.2.6)$$

A function $y(t) = (y_j(t))_{j \in \mathbb{Z}}$ with $y_j \in C^1([0, \infty), [0, 1])$ is called a lower solution of (4.2.2) if we have the reverse inequality

$$\frac{dy_j(t)}{dt} \leq (1 - y_j(t))\sigma\lambda \sum_{k=-\infty}^{\infty} y_{j-k}(t)p(k) - \mu y_j(t), \quad \forall t \geq 0, j \in \mathbb{Z}. \quad (4.2.7)$$

We also need the following assumption for the strong positivity of solutions.

(C1) $p(1) = p(-1) > 0$.

Theorem 4.2.2 Let $\hat{y} = \{\hat{y}_j\}_{j \in \mathbb{Z}}$ and $\bar{y} = \{\bar{y}_j\}_{j \in \mathbb{Z}}$ be a pair of lower and upper solutions of (4.2.2), respectively, with $\hat{y}_j, \bar{y}_j \in C^1([0, \infty), [0, 1])$ and $\hat{y}(0) \leq \bar{y}(0)$.

Then $\hat{y}(t) \leq \bar{y}(t), \forall t \geq 0$. If, in addition, condition (C1) holds, then $y^0 \in \mathbb{C}_1 \setminus \{0\}$ implies that $y(t, y^0) \gg 0, \forall t > 0$.

Proof. It is easy to see that $w_j(t) = \bar{y}_j(t) - \hat{y}_j(t), \forall j \in \mathbb{Z}, t \in [0, \infty)$, is continuous and bounded, and $w(t) := \inf_{j \in \mathbb{Z}} w_j(t)$ is continuous. To prove $\hat{y}(t) \leq \bar{y}(t), t \geq 0$, it suffices to prove $w(t) \geq 0, \forall t \geq 0$. Suppose the assertion is not true. Then there exists $t_0 > 0$ such that $w(t_0) < 0$ and

$$w(t_0)e^{-M_0 t_0} = \inf_{t \geq 0} w(t)e^{-M_0 t} < w(\tau)e^{-M_0 \tau}, \tau \in [0, t_0), \quad (4.2.8)$$

where M_0 is chosen to satisfy $M_0 > \sigma\lambda - \mu$.

Let $\{j_n\}_{n=1}^\infty$ be a sequence such that $w_{j_n}(t_0) < 0$ for all $n \geq 1$ and $\lim_{n \rightarrow \infty} w_{j_n}(t_0) = w(t_0)$. Let $\{t_n\}_{n=1}^\infty$ be a sequence in $(0, t_0]$ so that

$$w_{j_n}(t_n)e^{-M_0 t_n} = \min_{t \in [0, t_0]} w_{j_n}(t)e^{-M_0 t}. \quad (4.2.9)$$

For any $\epsilon \in (0, t_0)$, let $L_\epsilon := \min_{t \in [0, t_0 - \epsilon]} w(t)e^{-M_0 t}$. By (4.2.8), we have

$$\lim_{n \rightarrow \infty} w_{j_n}(t_0)e^{-M_0 t_0} = w(t_0)e^{-M_0 t_0} < L_\epsilon.$$

Thus, there is n_ϵ such that for all $n > n_\epsilon$,

$$w_{j_n}(t_0)e^{-M_0 t_0} < L_\epsilon \leq w(t)e^{-M_0 t} \leq w_{j_n}(t)e^{-M_0 t}, \forall t \in [0, t - \epsilon].$$

In view of (4.2.9), we obtain $t_n \in [t_0 - \epsilon, t_0], \forall n \geq n_\epsilon$, which implies that $\lim_{n \rightarrow \infty} t_n = t_0$.

Since

$$w_{j_n}(t_0)e^{-M_0 t_0} \geq w_{j_n}(t_n)e^{-M_0 t_n} \geq w(t_n)e^{-M_0 t_n} \geq w(t_0)e^{-M_0 t_0},$$

we have

$$w_{j_n}(t_0)e^{-M_0(t_0-t_n)} \geq w_{j_n}(t_n) \geq w(t_0)e^{-M_0(t_0-t_n)},$$

which yields to $\lim_{n \rightarrow \infty} w_{j_n}(t_n) = w(t_0)$. By (4.2.9), it follows that for each $n \geq 1$,

$$0 \geq \frac{d}{dt}\{w_{j_n}(t)e^{-M_0 t}\}|_{t=t_n} = e^{-M_0 t_n}(w'_{j_n}(t_n) - M_0 w_{j_n}(t_n)),$$

and hence, $w'_{j_n}(t_n) \leq M_0 w_{j_n}(t_n)$. Note that $w_{j_n}(t_n)$ satisfies

$$\begin{aligned} w'_{j_n}(t_n) &\geq (1 - \bar{y}_{j_n}(t_n))\sigma\lambda \sum_{k=-\infty}^{\infty} \bar{y}_{j_n-k}(t_n)p(k) - (1 - \hat{y}_{j_n}(t_n))\sigma\lambda \cdot \\ &\quad \sum_{k=-\infty}^{\infty} \hat{y}_{j_n-k}(t_n)p(k) - \mu w_{j_n}(t_n). \end{aligned}$$

Then for all sufficiently large n , we have

$$\begin{aligned} 0 &\leq w'_{j_n}(t_n) - (1 - \bar{y}_{j_n}(t_n))\sigma\lambda \sum_{k=-\infty}^{\infty} \bar{y}_{j_n-k}(t_n)p(k) + (1 - \hat{y}_{j_n}(t_n))\sigma\lambda \cdot \\ &\quad \sum_{k=-\infty}^{\infty} \hat{y}_{j_n-k}(t_n)p(k) + \mu w_{j_n}(t_n) \\ &\leq (\mu + M_0)w_{j_n}(t_n) - (1 - \bar{y}_{j_n}(t_n))\sigma\lambda \sum_{k=-\infty}^{\infty} \bar{y}_{j_n-k}(t_n)p(k) + (1 - \hat{y}_{j_n}(t_n))\sigma\lambda \\ &\quad \sum_{k=-\infty}^{\infty} \bar{y}_{j_n-k}(t_n)p(k) - (1 - \hat{y}_{j_n}(t_n))\sigma\lambda \sum_{k=-\infty}^{\infty} \bar{y}_{j_n-k}(t_n)p(k) + (1 - \hat{y}_{j_n}(t_n))\sigma\lambda \\ &\quad \sum_{k=-\infty}^{\infty} \hat{y}_{j_n-k}(t_n)p(k) \\ &= (\mu + M_0)w_{j_n}(t_n) + w_{j_n}(t_n)\sigma\lambda \sum_{k=-\infty}^{\infty} \bar{y}_{j_n-k}(t_n)p(k) - (1 - \hat{y}_{j_n}(t_n))\sigma\lambda \\ &\quad \sum_{k=-\infty}^{\infty} w_{j_n-k}(t_n)p(k) \\ &\leq -(1 - \hat{y}_{j_n}(t_n))\sigma\lambda w(t_n) + (\mu + M_0 + \sigma\lambda \sum_{k=-\infty}^{\infty} \bar{y}_{j_n-k}(t_n)p(k))w_{j_n}(t_n) \\ &\leq -\sigma\lambda w(t_n) + (\mu + M_0)w_{j_n}(t_n). \end{aligned}$$

Letting $n \rightarrow \infty$ in the above, we see that

$$(-\sigma\lambda + \mu + M_0)w(t_0) \geq 0.$$

Recalling that $\mu + M_0 - \sigma\lambda > 0$, we obtain that $w(t_0) \geq 0$, a contradiction. This shows that $w_j(t) = \bar{y}_j(t) - \hat{y}_j(t) \geq 0$ for all $j \in \mathbb{Z}$ and $t \in [0, \infty)$.

Next we prove the strong positivity of $y(t, y^0)$ under condition (C1). Since $y^0 \in \mathbb{C}_1 \setminus \{0\}$, there exists an integer $i \in \mathbb{Z}$ such that $y_i^0 > 0$. Note that $\sigma\lambda > 0$ and $p(1) = p(-1) > 0$. Clearly, we have

$$y_i(t) = e^{-\mu t} y_i(0) + \sigma\lambda \int_0^t e^{-\mu(t-s)} (1 - y_i(s)) \sum_{k=-\infty}^{\infty} y_k(s) p(i-k) ds > 0, \forall t > 0.$$

It then follows that

$$\begin{aligned} y_{i+1}(t) &= e^{-\mu t} y_{i+1}(0) + \sigma\lambda \int_0^t e^{-\mu(t-s)} (1 - y_{i+1}(s)) [y_i(s) p(1) \\ &\quad + \sum_{k \neq i, k=-\infty}^{\infty} y_k(s) p(i+1-k)] ds > 0, \forall t > 0, \end{aligned}$$

and

$$\begin{aligned} y_{i-1}(t) &= e^{-\mu t} y_{i-1}(0) + \sigma\lambda \int_0^t e^{-\mu(t-s)} (1 - y_{i-1}(s)) [y_i(s) p(-1) \\ &\quad + \sum_{k \neq i, k=-\infty}^{\infty} y_k(s) p(i-1-k)] ds > 0, \forall t > 0. \end{aligned} \tag{4.2.10}$$

Repeating this procedure, we have $y_{i+n}(t) > 0, y_{i-n}(t) > 0, \forall n \geq 0, \forall t > 0$, and hence, $y(t, y^0) \gg 0$ for all $t > 0$. ■

4.3 Spreading speed and traveling waves

In this section, we establish the existence of asymptotic spreading speed for system (4.2.2), and show that it coincides with the minimal wave speed for monotone traveling waves.

Note that if v is a solution of the scalar ordinary differential equation

$$\frac{dv(t)}{dt} = (\sigma\lambda - \mu - \sigma\lambda v(t)) v(t), \quad (4.3.11)$$

then $y_j = v, \forall j \in \mathbb{Z}$, is a solution of system (4.2.2). Throughout this section, we assume that

$$(C2) \quad \sigma\lambda > \mu.$$

Clearly, $\sigma\lambda - \mu - \sigma\lambda v = 0$ has a unique positive solution $v^* = \frac{\sigma\lambda - \mu}{\sigma\lambda} \in (0, 1]$. Let $\{Q_t\}_{t \geq 0}$ be the solution semiflow associated with system (4.2.2), that is,

$$Q_t(u) = y(t, u) = (y_j(t, u))_{j \in \mathbb{Z}}, \quad \forall u \in \mathbb{C}_{v^*}, t \geq 0.$$

Proposition 4.3.1 *For each $t > 0$, the map Q_t satisfies the hypothesis (A1)-(A5).*

Moreover, $\{Q_t\}_{t \geq 0}$ is a subhomogeneous semiflow on \mathbb{C}_{v^} .*

Proof. We only prove (A2) and (A5) since all the other conditions are easy to verify. We first prove continuity of $Q_t(u) = Q(t, u)$ in (t, u) . Let $y(t), \tilde{y}(t)$ be two solutions of (4.2.2) with $0 \leq y_j(t), \tilde{y}_j(t) \leq v^*, \forall j \in \mathbb{Z}$. Then the following statement is valid.

Claim 1. For any $\epsilon > 0, t_0 > 0$, there exist $\delta > 0$ and an integer $N > 0$ such that $|y_0(t) - \tilde{y}_0(t)| \leq \epsilon, \forall t \in [0, t_0]$, whenever $|y_j(0) - \tilde{y}_j(0)| < \delta$ for $-N \leq j \leq N$.

To prove this claim, we first consider the case that $y(0) \leq \tilde{y}(0)$. Then we have $y(t) \leq \tilde{y}(t), \forall t \in [0, \infty)$. Let $w(t) = \tilde{y}(t) - y(t)$ and $w_j^0 = \tilde{y}_j(0) - y_j(0)$. Then

$$\begin{aligned} & \frac{dw_j(t)}{dt} \\ &= \sigma \lambda \sum_{k=-\infty}^{+\infty} w_{j-k}(t) p(k) - \sigma \lambda \sum_{k=-\infty}^{+\infty} (\tilde{y}_j(t) \tilde{y}_{j-k}(t) - y_j(t) y_{j-k}(t)) p(k) - \mu w_j(t) \\ &= \sigma \lambda \sum_{k=-\infty}^{+\infty} w_{j-k}(t) p(k) - \sigma \lambda \sum_{k=-\infty}^{+\infty} (\tilde{y}_j(t) w_{j-k}(t) + w_j(t) y_{j-k}(t)) p(k) - \mu w_j(t) \\ &\leq \sigma \lambda \sum_{k=-\infty}^{+\infty} w_{j-k}(t) p(k) - \mu w_j(t). \end{aligned}$$

Next we consider the system

$$\begin{cases} \frac{d\bar{w}_j(t)}{dt} = \sigma \lambda \sum_{k=-\infty}^{+\infty} \bar{w}_{j-k}(t) p(k) - \mu \bar{w}_j(t) \\ \bar{w}_j(0) = w_j^0, \forall j \in \mathbb{Z}. \end{cases} \quad (4.3.12)$$

Using the discrete Fourier transform,

$$\begin{aligned} v(t, \tau) &= \frac{1}{\sqrt{2\pi}} \sum_{j=-\infty}^{+\infty} e^{-i(j\tau)} \bar{w}_j(t) \\ \bar{w}_j(t) &= \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{+\pi} e^{i(j\tau)} v(t, \tau) d\tau, \end{aligned}$$

where i is the imaginary unit, we have

$$\begin{aligned}
\frac{\partial v(t, \tau)}{\partial t} &= -\mu v(t, \tau) + \frac{\sigma \lambda}{\sqrt{2\pi}} \sum_{j=-\infty}^{+\infty} \sum_{k=-\infty}^{+\infty} e^{-i(j\tau)} \bar{w}_{j-k}(t) p(k) \\
&= -\mu v(t, \tau) + \frac{\sigma \lambda}{\sqrt{2\pi}} \sum_{k=-\infty}^{+\infty} \left(e^{-i(k\tau)} p(k) \sum_{j=-\infty}^{+\infty} \bar{w}_{j-k}(t) e^{-i(j-k)\tau} \right) \\
&= -\mu v(t, \tau) + \sigma \lambda v(t, \tau) \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} p(k) \\
&= (-\mu + \sigma \lambda \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} p(k)) v(t, \tau).
\end{aligned}$$

It then follows that

$$v(t, \tau) = \exp\left\{(-\mu + \sigma \lambda \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} p(k))t\right\} v(0, \tau),$$

with

$$v(0, \tau) = \frac{1}{\sqrt{2\pi}} \sum_{m=-\infty}^{+\infty} e^{-i(m\tau)} w_m^0.$$

Thus, we obtain

$$\begin{aligned}
\bar{w}_j(t) &= \frac{1}{2\pi} \int_{-\pi}^{\pi} \exp\{i(j\tau) + (-\mu + \sigma \lambda \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} p(k))t\} \sum_{m=-\infty}^{+\infty} e^{-i(m\tau)} w_m^0 d\tau \\
&= \frac{1}{2\pi} \sum_{m=-\infty}^{+\infty} \left(\int_{-\pi}^{\pi} \exp\{i(j-m)\tau + (-\mu + \sigma \lambda \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} p(k))t\} d\tau \right) w_m^0,
\end{aligned}$$

and hence,

$$w_j(t) \leq \frac{1}{2\pi} \sum_{m=-\infty}^{+\infty} \left(\int_{-\pi}^{\pi} \exp\{i(j-m)\tau + (-\mu + \sigma \lambda \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} p(k))t\} d\tau \right) w_m^0.$$

It is easy to see that for any $\epsilon > 0$ and $t_0 > 0$, there exist $\delta > 0$ and an integer

$N > 0$ such that $w_0(t) \leq \epsilon, \forall t \in [0, t_0]$, whenever $w_j(0) < \delta$ for $-N \leq j \leq N$.

Regarding the case that $y(0) \not\leq \tilde{y}(0)$, let $\tilde{z}(t), z(t)$ be two solutions of (4.2.2) with $\tilde{z}_j(0) = \max\{y_j(0), \tilde{y}_j(0)\}, z_j(0) = \min\{y_j(0), \tilde{y}_j(0)\}, \forall j \in \mathbb{Z}$. Since $z(0) \leq \tilde{z}(0)$, we have

$$|y_j(t) - \tilde{y}_j(t)| \leq |\tilde{z}_j(t) - z_j(t)| < \epsilon, \quad \forall t \in [0, t_0],$$

whenever $|y_j(0) - \tilde{y}_j(0)| = |\tilde{z}_j(0) - z_j(0)| < \delta, \forall j \in \mathbb{Z}$. This proves the claim.

Claim 2. For any $t_0 > 0$, $Q_t(u)$ is continuous in u uniformly for $t \in [0, t_0]$.

Fix \bar{u} and $t_0 > 0$. By Claim 1, it follows that for any $\epsilon > 0$, there are δ and N such that

$$|y_{j_0}(t, u) - y_{j_0}(t, \bar{u})| < \frac{1}{4}\epsilon, \quad (4.3.13)$$

whenever $|u_j - \bar{u}_j| < \delta, \forall j_0 - N \leq j \leq j_0 + N$ for some $j_0 \in \mathbb{Z}$. Choose $m > 0$ such that $\sum_{k=m+1}^{\infty} \frac{2v^*}{2^k} < \frac{\epsilon}{2}$, and let $\delta_1 = 2^{-(m+N)}\delta$. For any $u \in \mathbb{C}_v$ with $d(u, \bar{u}) = \sum_{k=0}^{\infty} \frac{\max_{-k \leq j \leq k} |u_j - \bar{u}_j|}{2^k} < \delta_1$, we have

$$\max_{-(m+N) \leq j \leq m+N} |u_j - \bar{u}_j| < 2^{m+N}\delta_1 := \delta.$$

By (4.3.13), it follows that

$$|y_{j_0}(t, u) - y_{j_0}(t, \bar{u})| < \frac{1}{4}\epsilon, \quad \forall j_0 \in [-m, m],$$

and hence,

$$\begin{aligned} d(y(t, u), y(t, \bar{u})) &\leq \max_{-m \leq j \leq m} |y_j(t, u) - y_j(t, \bar{u})| \sum_{k=0}^m \frac{1}{2^k} + \sum_{k=m+1}^{\infty} \frac{2v^*}{2^k} \\ &< \frac{\epsilon}{4} \sum_{k=0}^{\infty} \frac{1}{2^k} + \frac{\epsilon}{2} = \epsilon, \end{aligned}$$

whenever $d(u, \bar{u}) < \delta_1$.

Consequently, $Q_t(u) = Q(t, u)$ is continuous in $(t, u) \in \mathbb{R}_+ \times \mathbb{C}_{v^*}$ with respect to the compact open topology.

Note that system (4.3.11) has two equilibria 0 and v^* , and v^* is a globally asymptotically stable equilibrium in $(0, v^*]$. By Theorem 1.2.1, there exists an entire strictly increasing orbit such that $\lim_{t \rightarrow -\infty} v(t) = 0$ and $\lim_{t \rightarrow \infty} v(t) = v^*$. Thus, (A5) is satisfied.

Finally, we show that Q_t is subhomogeneous in the sense that $Q_t(\kappa y^0) \geq \kappa Q_t(y^0)$ for any $0 \leq \kappa \leq 1$ and $y^0 \in \mathbb{C}_{v^*}$. Since

$$\begin{aligned} \frac{d(\kappa y_j(t))}{dt} &= (1 - y_j(t))\sigma\lambda \sum_{k=-\infty}^{\infty} \kappa y_{j-k}(t)p(k) - \mu\kappa y_j(t) \\ &\leq (1 - \kappa y_j(t))\sigma\lambda \sum_{k=-\infty}^{\infty} \kappa y_{j-k}(t)p(k) - \mu\kappa y_j(t), \quad j \in \mathbb{Z}, \end{aligned}$$

$\kappa y(t, y^0)$ is a lower solution of (4.2.2) with initial value κy^0 . By the comparison theorem, we thus have $\kappa y(t, y^0) \leq y(t, \kappa y^0)$ for all $t \geq 0$. \blacksquare

Let c^* be the asymptotic speed of spread of the map Q_1 on \mathbb{C}_{v^*} . In order to compute c^* , we consider the linearized equation (4.2.2) at $y = 0$,

$$\frac{dy_j(t)}{dt} = \sigma\lambda \sum_{k=-\infty}^{+\infty} y_{j-k}(t)p(k) - \mu y_j(t). \quad (4.3.14)$$

Let $\{M_t\}_{t \geq 0}$ be the solution semiflow associated with system (4.3.14). Note that $Q_t(y^0)$ is a lower solution of the linear system (4.3.14) for $t \in [0, \infty)$. It then follows that

$$Q_t(y^0) \leq M_t(y^0), \forall y^0 \in \mathbb{C}_{v^*}, \forall t \geq 0.$$

For each $u_0 \in \mathbb{R}$, let $\eta(t, u^0)$ be the unique solution of the linear equation

$$\frac{d\eta(t)}{dt} = \sigma \lambda \eta(t) \sum_{k=-\infty}^{+\infty} e^{\chi k} p(k) - \mu \eta(t), \quad (4.3.15)$$

with $\eta(0, u^0) = u^0$. It is easy to see that $y(t) = \{y_j(t)\}_{j \in \mathbb{Z}}$ with $y_j(t) = e^{-\chi j} \eta(t, u^0)$ is a solution of (4.3.14). Thus we have $B_\chi^t(u^0) := M_t(e^{-\chi \cdot} u^0)(0) = \eta(t, u^0)$, which implies that B_χ^t is the solution map of (4.3.15). Note that the general solution of (4.3.15) is

$$\eta(t, u^0) = \exp\left\{(\sigma \lambda \sum_{k=-\infty}^{+\infty} e^{\chi k} p(k) - \mu)t\right\} u^0.$$

Then $B_\chi^t(u^0) = \exp\left\{(\sigma \lambda \sum_{k=-\infty}^{+\infty} e^{\chi k} p(k) - \mu)t\right\} u^0$, and $\exp\left\{(\sigma \lambda \sum_{k=-\infty}^{+\infty} e^{\chi k} p(k) - \mu)t\right\}$ is the principal eigenvalue of B_χ^t with the positive eigenfunction u^0 . When $\chi = 0$, we have the principal eigenvalue $\exp\{(\sigma \lambda - \mu)t\} > 1$. Thus the map M_t satisfies the assumptions (B1)-(B7) for each $t > 0$.

Letting $t = 1$, we see that $\lambda(\chi) := \exp\left\{\sigma \lambda \sum_{k=-\infty}^{+\infty} e^{\chi k} p(k) - \mu\right\}$ is the principal eigenvalue of B_χ^1 . Define the function

$$\Phi(\chi) := \frac{1}{\chi} \ln \lambda(\chi) = \frac{\sigma \lambda \sum_{k=-\infty}^{+\infty} e^{\chi k} p(k) - \mu}{\chi}. \quad (4.3.16)$$

Since $\Phi(\chi) \rightarrow \infty$ as $\chi \rightarrow 0$, and $p(k_0) > 0$ for some $k_0 > 0$, we have $\Phi(\chi) \geq \frac{\sigma \lambda e^{\chi k_0} p(k_0) - \mu}{\chi} \rightarrow \infty$ as $\chi \rightarrow \infty$. $\Phi(\chi)$ then assumes its minimum at some finite value χ^* . Since $Q_1(y^0) \leq M_1(y^0)$, $\forall y^0 \in \mathbb{C}_v^*$, Theorem 1.3.1 implies that $c^* \leq \inf_{\chi > 0} \Phi(\chi)$.

Consider the linear system

$$\frac{dy_j(t)}{dt} = \sigma \lambda (1 - \epsilon) \sum_{k=-\infty}^{+\infty} y_{j-k}(t) p(k) - \mu y_j(t) \quad (4.3.17)$$

with parameter ϵ . Let $\{M_t^\epsilon\}_{t \geq 0}$ be the solution semiflow associated with system (4.3.17). For any $0 < \epsilon < 1$, there is $\delta \in (0, \epsilon)$ such that $0 \leq y_j(t) \leq v(t, \delta) < \epsilon, \forall j \in \mathbb{Z}, \forall t \in [0, 1]$, provided $0 \leq y_j(0) \leq \delta, \forall j \in \mathbb{Z}$, where $v(t, \delta)$ is the solution of (4.3.11) satisfying $v(0, \delta) = \delta$. Thus, $Q_t(y^0)$ is an upper solution of linear system (4.3.17) for $t \in [0, 1]$. It then follows that $Q_t(y^0) \geq M_t^\epsilon(y^0), \forall y^0 \in \mathbb{C}_\delta, \forall t \in [0, 1]$. In particular, $Q_1(y^0) \geq M_1^\epsilon(y^0)$. As we did for $\{M_t\}_{t \geq 0}$, similar analysis can be carried out for $\{M_t^\epsilon\}_{t \geq 0}$. By Theorem 1.3.1, we have

$$\inf_{\chi > 0} \Phi_\epsilon(\chi) \leq c^* \leq \inf_{\chi > 0} \Phi(\chi), \quad \forall \epsilon \in (0, 1).$$

Letting $\epsilon \rightarrow 0$, we obtain

$$c^* = \inf_{\chi > 0} \Phi(\chi) = \Phi(\chi^*).$$

The following result shows that the above-defined c^* is the spreading speed for solutions of (4.2.2) with initial data having compact supports.

Theorem 4.3.1 *Assume that (C2) holds. Let $y(t)$ be a solution of (4.2.2) with $y(0) \in \mathbb{C}_{v^*}$. Then the following statements are valid:*

(1) *For any $c > c^*$, if $y(0) \ll v^*$ and $y_j(0) = 0$ for j outside a bounded interval, then*

$$\lim_{t \rightarrow \infty, |j| \geq ct} y_j(t) = 0.$$

(2) *For any $c \in (0, c^*)$, there is an $r > 0$ such that if $y_j(0) > 0$ for j on an interval*

$$\text{of length } 2r, \text{ then } \lim_{t \rightarrow \infty, |j| \leq ct} y_j(t) = v^*.$$

(3) *If, in addition, (C1) holds, then $y(0) \neq 0$ implies that $\lim_{t \rightarrow \infty, |j| \leq ct} y_j(t) = v^*$ for any $c \in (0, c^*)$.*

Proof. Conclusion (1) is a straightforward consequence of the first part of Theorem 1.3.2. For any given $c < c^*$, since Q_1 is subhomogeneous, the positive number r_α defined in Theorem 1.3.2 can be chosen to be independent of $\alpha \gg 0$. Let $r_\alpha = r$. If there is an $r > 0$ such that $y_j(0) > 0$ for j on an interval of length $2r$, then there exist $\alpha > 0$ such that $y_j(0) > \alpha$ for all j in this interval. Thus, conclusion (2) follows from the second part of Theorem 1.3.2. If, in addition, (C1) holds, then Theorem 4.2.2 implies that $y_j(t) > 0, \forall j \in \mathbb{Z}, \forall t > 0$. Fix a $t_0 > 0$, we have $y_j(t_0) > 0, \forall j \in \mathbb{Z}$. Taking $(y_j(t_0))_{j \in \mathbb{Z}}$ as a new initial value, we then obtain conclusion (3) from (2). ■

The existence and nonexistence of traveling wave solutions are straightforward consequences of Theorem 1.3.3.

Theorem 4.3.2 *Assume that (C2) holds. Then the following two statements are valid:*

- (1) *For any $c \in (0, c^*)$, (4.2.2) has no traveling wave $U(j - ct)$ connecting v^* to 0.*
- (2) *For any $c \geq c^*$, (4.2.2) has a traveling wave $U(j - ct)$ connecting v^* to 0 such that $U(s)$ is continuous and non-increasing in $s \in \mathbb{R}$.*

4.4 Multi-population case

In this section, we extend the results in the previous sections to the multi-population model

$$\begin{aligned} \frac{dy_{j,m}(t)}{dt} = & (1 - y_{j,m}(t)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} y_{j-k,n}(t) p_{mn}(k) - \mu_m y_{j,m}(t), \\ & j \in \mathbb{Z}, \quad 1 \leq m \leq r, \end{aligned} \quad (4.4.18)$$

where $y_j(t) = (y_{j,m}(t))_{m=1}^r$, $\alpha_{mn} = \sigma_n \lambda_{mn}$. We assume that

(D1) the matrix $\Lambda = (\alpha_{mn})_{r \times r}$ is irreducible in the sense that for any given index

$1 \leq i \neq j \leq r$, there is a finite sequence with distinct elements i_1, \dots, i_h , such

that $i_1 = i, i_h = j$ and $\alpha_{i_s i_{s+1}} > 0, \forall 1 \leq s \leq h-1$.

4.4.1 Existence and comparison of solutions

In this subsection, we show the existence and uniqueness of the solutions of (4.4.18).

Let $\bar{1}$ be the r -dimensional vector with each element being 1.

Theorem 4.4.1 *For any $y^0 \in \mathbb{C}_{\bar{1}}$, (4.4.18) has a unique continuous solution $y(t, y^0)$ on $[0, \infty)$ such that $y(0, y^0) = y^0$ and $y(t, y^0) \in \mathbb{C}_{\bar{1}}, \forall t \geq 0$.*

Proof. We first choose a sufficiently large number $D_m \geq \sum_{n=1}^r \alpha_{mn}, 1 \leq m \leq r$ such that

$$F_{j,m}(y) = (1 - y_{j,m}) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} y_{j-k,n} p_{mn}(k) + D_m y_{j,m}, j \in \mathbb{Z}, 1 \leq m \leq r,$$

is a monotone increasing mapping from \mathbb{C}_1 to \mathbb{R} . Clearly, (4.4.18) can be written as

$$\frac{dy_{j,m}(t)}{dt} = F_{j,m}(y) - (\mu_m + D_m)y_{j,m}(t), \quad j \in \mathbb{Z}, \quad 1 \leq m \leq r. \quad (4.4.19)$$

The initial problem of (4.4.19) is equivalent to

$$\begin{cases} y_{j,m}(t) = e^{-(\mu_m + D_m)t} y_{j,m}(0) + \int_0^t e^{-(\mu_m + D_m)(t-s)} F_{j,m}(y) ds, \forall j \in \mathbb{Z}, 1 \leq m \leq r, \\ y(0) = y^0. \end{cases} \quad (4.4.20)$$

For any $y^0 \in \mathbb{C}_1$, and any $T \in (0, \infty)$, define

$$S_T := \{y = \{y_j\}_{j \in \mathbb{Z}} : y_j \in C([0, T], [0, 1]^r), y(0) = y^0, \forall j \in \mathbb{Z}\},$$

and an operator $H^T = \{H_j^T\}_{j \in \mathbb{Z}}$ by $\{H_j^T\} = \{H_{j,m}^T\}_{1 \leq m \leq r}$ on S_T , with

$$\begin{aligned} H_{j,m}^T(y)(t) &= e^{-(\mu_m + D_m)t} y_{j,m}(0) + \int_0^t e^{-(\mu_m + D_m)(t-s)} F_{j,m}(y) ds, \\ &\forall y \in S_T, \forall j \in \mathbb{Z}, 1 \leq m \leq r. \end{aligned}$$

Since

$$\begin{aligned} 0 \leq H_{j,m}^T(y)(t) &\leq e^{-(\mu_m + D_m)t} + F_{j,m}(1) \int_0^t e^{-(\mu_m + D_m)(t-s)} ds \\ &= \frac{D_m}{\mu_m + D_m} + e^{-(\mu_m + D_m)t} \frac{\mu_m}{\mu_m + D_m} \leq 1, \forall t \in [0, T], \end{aligned} \quad (4.4.21)$$

we have $H^T(S_T) \subseteq S_T$. For any $\beta > 0$, we define

$$\|y\|_\beta := \sup_{t \in [0, T], j \in \mathbb{Z}, 1 \leq m \leq r} |y_{j,m}(t)| e^{-\beta t}, \forall y \in S_T.$$

Then $(S_T, \|\cdot\|)$ is a Banach space. For any $y, \bar{y} \in S_T$, let $w = \{w_j\}_{j \in \mathbb{Z}}$ with $w_j = \bar{y}_j - y_j$.

It follows that

$$\begin{aligned}
& H_{j,m}^T(\bar{y})(t) - H_{j,m}^T(y)(t) \\
&= \int_0^t e^{-(\mu_m + D_m)(t-s)} (F_{j,m}(\bar{y}(s)) - F_{j,m}(y(s))) ds \\
&= \int_0^t e^{-(\mu_m + D_m)(t-s)} [D_m w_{j,m}(s) + (1 - \bar{y}_{j,m}(s)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \sigma_n \lambda_{m,n} \bar{y}_{j-k,n}(s) p(k) \\
&\quad - (1 - y_{j,m}(s)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \sigma_n \lambda_{m,n} y_{j-k,n}(s) p(k)] ds \\
&= \int_0^t e^{-(\mu_m + D_m)(t-s)} [D_m w_{j,m}(s) + \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \sigma_n \lambda_{m,n} p(k) (w_{j-k,n}(s) - \bar{y}_{j-k,n}(s) w_{j,m} \\
&\quad - y_{j,m}(s) w_{j-k,n})] ds,
\end{aligned}$$

which leads to

$$\begin{aligned}
& |H_{j,m}^T(\bar{y})(t) - H_{j,m}^T(y)(t)| e^{-\beta t} \\
&\leq \int_0^t e^{-\beta(t-s)-\beta s} [D_m |w_{j,m}(s)| + \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \sigma_n \lambda_{m,n} p(k) (|w_{j-k,n}(s)| + \bar{y}_{j-k,n}(s) \\
&\quad |w_{j,m}(s)| + y_{j,m}(s) |w_{j-k,n}(s)|)] ds \\
&\leq \int_0^t e^{-\beta(t-s)-\beta s} [D_m |w_{j,m}(s)| + \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \sigma_n \lambda_{m,n} p(k) (2|w_{j-k,n}(s)| + |w_{j,m}(s)|)] ds.
\end{aligned}$$

Thus we have

$$\begin{aligned}
& \|H^T(\bar{y}) - H^T(y)\|_\beta \\
&= \sup_{t \in [0, T], j \in \mathbb{Z}, 1 \leq m \leq r} |H_{j,m}^T(\bar{y})(t) - H_{j,m}^T(y)(t)| e^{-\beta t} \\
&\leq \sup_{s \in [0, T], j \in \mathbb{Z}, 1 \leq m \leq r} |w_{j,m}(s)| e^{-\beta s} \cdot \sup_{t \in [0, T], 1 \leq m \leq r} \int_0^t e^{-\beta(t-s)} [D_m + \sum_{k=-\infty}^{\infty} \sum_{n=1}^r 3\sigma_n \lambda_{m,n} p(k)] ds \\
&\leq \frac{3 \sum_{n=1}^r \sigma_n \lambda_{m,n} + D_m}{\beta} (1 - e^{-\beta T}) \|\bar{y} - y\|_\beta.
\end{aligned}$$

Since

$$\lim_{\beta \rightarrow \infty} \frac{3 \sum_{n=1}^r \sigma_n \lambda_{m,n} + D_m}{\beta} (1 - e^{-\beta T}) = 0, \quad (4.4.22)$$

it follows that for sufficiently large β , H^T is a contraction on S_T , and hence, H^T has a unique fixed point y in S_T . This shows that system (4.4.18) has a unique solution on $[0, T]$, $\forall T \in (0, \infty)$, which implies the uniqueness and existence of a solution $y(t)$ of (4.4.18) on $[0, \infty)$. ■

Similar to Definition 4.2.1, we can define upper and lower solutions of system (4.4.18). In order to prove the strong positivity of solutions, we need the following assumption.

(D2) $p_{mn}(1) = p_{mn}(-1) > 0$ and $p_{mn}(0) > 0$ whenever $1 \leq m, n \leq r$ with $\alpha_{mn} > 0$.

Theorem 4.4.2 *Let $\hat{y} = \{\hat{y}_j\}_{j \in \mathbb{Z}}$ and $\bar{y} = \{\bar{y}_j\}_{j \in \mathbb{Z}}$ be a pair of lower and upper solution of (4.4.18), respectively, with $\hat{y}_j, \bar{y}_j \in C^1([0, \infty), [0, 1]^r)$ and $\hat{y}(0) \leq \bar{y}(0)$.*

Then $\hat{y}(t) \leq \bar{y}(t), \forall t \geq 0$. If, in addition, condition (D2) holds, then $y^0 \in \mathbb{C}_I \setminus \{0\}$ implies that $y(t, y^0) \gg 0, \forall t > 0$.

Proof. It is easy to see that $w_j(t) = \bar{y}_j(t) - \hat{y}_j(t), \forall j \in \mathbb{Z}, t \in [0, \infty)$, is continuous and bounded, and $w(t) := \min_{1 \leq m \leq r} \inf_{j \in \mathbb{Z}} w_{j,m}(t)$ is continuous. To prove $\hat{y}(t) \leq \bar{y}(t), t \geq 0$, it suffices to prove $w(t) \geq 0, \forall t \geq 0$. Suppose the assertion is not true. Then there exists $t_0 > 0$ such that $w(t_0) < 0$ and

$$w(t_0)e^{-M_0 t_0} = \min_{t \in [0, t_0]} w(t)e^{-M_0 t} < w(\tau)e^{-M_0 \tau}, \tau \in [0, t_0), \quad (4.4.23)$$

where M_0 is chosen such that

$$M_0 > \max_{1 \leq m \leq r} (-\mu_m + \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn}) > 0. \quad (4.4.24)$$

Hence, there exist a sequence j_s and an index m such that $w_{j_s, m}(t_0) < 0$ for all $s \geq 1$ and $\lim_{s \rightarrow \infty} w_{j_s, m}(t_0) = w(t_0)$. Let $\{t_s\}_{s=1}^{\infty}$ be a sequence in $[0, t_0]$ such that

$$w_{j_s, m}(t_s)e^{-M_0 t_s} = \min_{t \in [0, t_0]} w_{j_s, m}(t)e^{-M_0 t}. \quad (4.4.25)$$

For any $\epsilon \in (0, t_0)$, let $L_\epsilon := \min_{t \in [0, t_0 - \epsilon]} w(t)e^{-M_0 t}$. By (4.4.23), we have

$$\lim_{s \rightarrow \infty} w_{j_s, m}(t_0)e^{-M_0 t_0} = w(t_0)e^{-M_0 t_0} < L_\epsilon.$$

Thus, there is s_ϵ such that for all $s > s_\epsilon$,

$$w_{j_s, m}(t_0)e^{-M_0 t_0} < L_\epsilon \leq w(t)e^{-M_0 t} \leq w_{j_s, m}(t)e^{-M_0 t}, \forall t \in [0, t_0 - \epsilon].$$

In view of (4.4.25), we obtain $t_s \in [t_0 - \epsilon, t_0], \forall s \geq s_\epsilon$, which implies that $\lim_{s \rightarrow \infty} t_s = t_0$.

Since

$$w_{j_s, m}(t_0)e^{-M_0 t_0} \geq w_{j_s, m}(t_s)e^{-M_0 t_s} \geq w(t_s)e^{-M_0 t_s} \geq w(t_0)e^{-M_0 t_0},$$

we have

$$w_{j_s,m}(t_0)e^{-M_0(t_0-t_s)} \geq w_{j_s,m}(t_s) \geq w(t_0)e^{-M_0(t_0-t_s)},$$

which yields to $\lim_{s \rightarrow \infty} w_{j_s,m}(t_s) = w(t_0)$.

By (4.4.25), it follows that for each $s \geq 1$ such that

$$0 \geq \frac{d}{dt} \{w_{j_s,m}(t)e^{-M_0 t}\} \big|_{t=t_s^-} = e^{-M_0 t_s} (w'_{j_s,m}(t_s) - M_0 w_{j_s,m}(t_s))$$

and hence, $w'_{j_s,m}(t_s) \leq M_0 w_{j_s,m}(t_s)$. Note that $w_{j_s,m}(t_s)$ satisfies

$$\begin{aligned} w'_{j_s,m}(t_s) &\geq (1 - \bar{y}_{j_s,m}(t_s)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} \bar{y}_{j_s-k,n}(t_s) p_{mn}(k) - (1 - \hat{y}_{j_s,m}(t_s)) \\ &\quad \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} \hat{y}_{j_s-k,n}(t_s) p_{mn}(k) - \mu_m w_{j_s,m}(t_s). \end{aligned}$$

Then for all sufficiently large s , we have

$$\begin{aligned} 0 &\leq w'_{j_s,m}(t_s) - \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} p_{mn}(k) [\bar{y}_{j_s-k,n}(t_s)(1 - \bar{y}_{j_s,m}(t_s)) - \hat{y}_{j_s-k,n}(t_s) \\ &\quad (1 - \hat{y}_{j_s,m}(t_s))] + \mu_m w_{j_s,m}(t_s) \\ &\leq (\mu_m + M_0) w_{j_s,m}(t_s) + \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} p_{mn}(k) [\bar{y}_{j_s-k,n}(t_s) w_{j_s,m}(t_s) - w_{j_s-k,m}(t_s) \\ &\quad (1 - \hat{y}_{j_s,m}(t_s))] \\ &\leq [\mu_m + M_0 + \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} \bar{y}_{j_s-k,n}(t_s) p_{mn}(k)] w_{j_s,m}(t_s) - \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} \\ &\quad w_{j_s-k,m}(t_s) (1 - \hat{y}_{j_s,n}(t_s)) \\ &\leq - \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} w(t_s) + (\mu_m + M_0) w_{j_s,m}(t_s). \end{aligned}$$

Letting $s \rightarrow \infty$ in the above inequality, we obtain

$$(\mu_m + M_0 - \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn}) w(t_0) \geq 0.$$

By (4.4.24), it follows that $w(t_0) \geq 0$, a contradiction. This shows that $w_{j,m}(t) = \bar{y}_{j,m}(t) - \hat{y}_{j,m}(t) \geq 0$ for all $j \in \mathbb{Z}$, $1 \leq m \leq r$, and $t \in [0, \infty)$.

Next we show the strong positivity of solutions under condition (D2). Since $y^0 \in \mathbb{C}_1 \setminus \{0\}$, there exist two integers $j \in \mathbb{Z}$ and $1 \leq l \leq r$ such that $y_{j,l}^0 > 0$. It is easy to see that

$$\begin{aligned} y_{j,l}(t) &= \int_0^t [e^{-\mu_l(t-s)}(1 - y_{j,l}(s)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{ln} y_{j-k,n}(s) p_{ln}(k)] ds \\ &\quad + e^{-\mu_l t} y_{j,l}(0) \\ &> 0. \end{aligned}$$

By assumptions (D1) and (D2), for any $q \neq l$, there is a finite sequence with distinct elements i_1, \dots, i_h , such that $i_1 = q, i_h = l$, $\alpha_{i_s, i_{s+1}} > 0, \forall 1 \leq s \leq h-1$, and hence, $p_{i_s, i_{s+1}}(1) = p_{i_s, i_{s+1}}(-1) > 0, p_{i_s, i_{s+1}}(0) > 0$. Thus, we obtain

$$\begin{aligned} y_{j, i_{h-1}}(t) &= e^{-\mu_{i_{h-1}} t} y_{j, i_{h-1}}(0) + \int_0^t e^{-\mu_{i_{h-1}}(t-s)} (1 - y_{j, i_{h-1}}(s)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{i_{h-1}, n} \\ &\quad y_{j-k, n}(s) p_{i_{h-1}, n}(k) ds \\ &\geq \int_0^t e^{-\mu_{i_{h-1}}(t-s)} (1 - y_{j, i_{h-1}}(s)) \alpha_{i_{h-1}, m} y_{j, m}(s) p_{i_{h-1}, m}(0) ds \\ &> 0. \end{aligned}$$

Similarly, we have

$$y_{j, i_{h-2}}(t) > 0.$$

Repeating these procedures, we obtain

$$y_{j, q}(t) > 0, \forall t > 0,$$

which implies that $y_{j,m}(t) > 0, \forall 1 \leq m \leq r, t > 0$. For any $1 \leq m \leq r$, there is at least one $n \neq m$ such that $\alpha_{mn} > 0$ and $p_{mn}(1) = p_{mn}(-1) > 0$, and hence, we have

$$\begin{aligned} y_{j+1,m}(t) &= e^{-\mu_m t} y_{j+1,m}(0) + \int_0^t [e^{-\mu_m(t-s)} (1 - y_{j+1,m}(s)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} y_{j+1-k,n}(s) \\ &\quad p_{mn}(k)] ds \\ &\geq \int_0^t e^{-\mu_m(t-s)} (1 - y_{j+1,m}(s)) \sum_{n=1}^r \alpha_{mn} y_{j,n}(s) p_{mn}(1) ds \\ &> 0. \end{aligned}$$

Similarly, we find

$$y_{j-1,m}(t) > 0.$$

Continuing this procedure, we obtain

$$y_{j+n,m}(t) > 0, \forall n \in \mathbb{Z}, 1 \leq m \leq r, t > 0.$$

Thus, $y(t, y^0) \gg 0$ for all $t > 0$. ■

4.4.2 Spreading speed and traveling waves

In this subsection, we establish the existence of the asymptotic spreading speed for system (4.4.18), and show that it coincides with the minimal wave speed for monotone traveling waves.

Note that if $v = \{v_m\}_{m=1}^r$ is a solution of

$$\frac{dv_m(t)}{dt} = (1 - v_m(t)) \sum_{n=1}^r \alpha_{mn} v_n(t) - \mu_m v_m(t), \quad 1 \leq m \leq r, \quad (4.4.26)$$

then $y_j = v, \forall j \in \mathbb{Z}$, is a solution of system (4.4.18). If $\mu = (\mu_1, \mu_2, \dots, \mu_r) \gg 0$, then we define $\Gamma := (\text{diag}(\mu))^{-1}\Lambda$, and let $\rho(\Gamma)$ be the spectral radius of the matrix Γ . Throughout this section, we assume that

(D3) Either $\mu_i = 0$ for some $1 \leq i \leq r$, or $\mu \gg 0$ and $\rho(\Gamma) > 1$.

By [41, Theorem 8.4](see also [64, Corollary 3.2]), system (4.4.26) has a globally asymptotically stable equilibrium $v^* = \{v_m^*\}_{m=1}^r \gg 0$ in $[0, 1]^r \setminus \{0\}$. Let $\{Q_t\}_{t \geq 0}$ be the solution semiflow associated with system (4.4.18), that is,

$$Q_t(u) = y(t, u) = (y_m(t, u))_{m=1}^r, \quad \forall u \in \mathbb{C}_{v^*}, t \geq 0.$$

Proposition 4.4.1 *For each $t > 0$, the map Q_t satisfies the hypothesis (A1)-(A5).*

Moreover, $\{Q_t\}_{t \geq 0}$ is a subhomogeneous semiflow on \mathbb{C}_{v^} .*

Proof. We only prove the conditions (A2) and (A5) since all the other conditions are easy to verify. We first establish the continuity of $Q_t(u) = Q(t, u)$ in (t, u) . Let $y(t), \tilde{y}(t)$ be two solutions of (4.4.18) with $0 \leq y_j(t), \tilde{y}_j(t) \leq v^*, \forall j \in \mathbb{Z}$. Then we have the following claim.

Claim 1. For any $\epsilon > 0, t_0 > 0$, there exist $\delta > 0$ and an integer $N > 0$ such that $\|y_0(t) - \tilde{y}_0(t)\| \leq \epsilon, \forall t \in [0, t_0]$, whenever $\|y_j(0) - \tilde{y}_j(0)\| < \delta, \forall -N \leq j \leq N$.

To prove this claim, we first consider the case that $y(0) \leq \tilde{y}(0)$. Then we have $y(t) \leq \tilde{y}(t), \forall t \in [0, \infty)$. Let $w_{j,m}(t) = \tilde{y}_{j,m}(t) - y_{j,m}(t)$ and $w_{j,m}^0 = \tilde{y}_{j,m}(0) - y_{j,m}(0)$.

Then

$$\begin{aligned}
\frac{dw_{j,m}(t)}{dt} &= (1 - \tilde{y}_{j,m}(t)) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} \tilde{y}_{j-k,n}(t) p_{mn}(k) - (1 - y_{j,m}(t)) \\
&\quad \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} y_{j-k,n}(t) p_{mn}(k) - \mu_m w_{j,m}(t) \\
&= \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} w_{j-k,n}(t) p_{mn}(k) + \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} (y_{j,m}(t) y_{j-k,n}(t) \\
&\quad - \tilde{y}_{j,m}(t) \tilde{y}_{j-k,n}(t)) p_{mn}(k) - \mu_m w_{j,m}(t) \\
&\leq \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} w_{j-k,n}(t) p_{mn}(k) - \mu_m w_{j,m}(t).
\end{aligned}$$

Next we consider the system

$$\begin{cases} \frac{d\bar{w}_{j,m}(t)}{dt} = \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} \bar{w}_{j-k,n}(t) p_{mn}(k) - \mu_m \bar{w}_{j,m}(t) \\ \bar{w}_{j,m}(0) = w_{j,m}^0, \forall j \in \mathbb{Z}, 1 \leq m \leq r. \end{cases} \quad (4.4.27)$$

Using the discrete Fourier transform,

$$\begin{aligned}
v_m(t, \tau) &= \frac{1}{\sqrt{2\pi}} \sum_{j=-\infty}^{+\infty} e^{-i(j\tau)} \bar{w}_{j,m}(t) \\
\bar{w}_{j,m}(t) &= \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{+\pi} e^{i(j\tau)} v_m(t, \tau) d\tau,
\end{aligned}$$

where i is the imaginary unit, we have

$$\begin{aligned}
\frac{\partial v_m(t, \tau)}{\partial t} &= \frac{1}{\sqrt{2\pi}} \sum_{j=-\infty}^{+\infty} e^{-i(j\tau)} [-\mu_m \bar{w}_{j,m}(t) + \sum_{k=-\infty}^{+\infty} \sum_{n=1}^r \alpha_{mn} \bar{w}_{j-k,n}(t) p_{mn}(k)] \\
&= -\mu_m v_m(t, \tau) + \sum_{n=1}^r \alpha_{mn} \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} p_{mn}(k) v_n(t, \tau).
\end{aligned}$$

We can write this equation as $\frac{dv(t,\tau)}{dt} = Bv$, where

$$B = \begin{pmatrix} -\mu_1 + \gamma_{11} & \gamma_{12} & \cdots & \gamma_{1r} \\ \vdots & \vdots & \ddots & \vdots \\ \gamma_{r1} & \gamma_{r2} & \cdots & -\mu_r + \gamma_{rr} \end{pmatrix},$$

with $\gamma_{ij} = \alpha_{ij} \sum_{k=-\infty}^{\infty} e^{-i(k\tau)} p_{ij}(k)$. The general solution of this equation can be written as

$$v(t, \tau) = e^{Bt} v(0, \tau),$$

with

$$v(0, \tau) = \begin{pmatrix} \frac{1}{\sqrt{2\pi}} \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} w_{k,1}^0 \\ \vdots \\ \frac{1}{\sqrt{2\pi}} \sum_{k=-\infty}^{+\infty} e^{-i(k\tau)} w_{k,r}^0 \end{pmatrix}.$$

Since $e^{Bt}v(0, \tau)$ is a $r \times 1$ matrix, we denote by $(e^{Bt}v(0, \tau))_m$ the m th row of this matrix. Thus, we have

$$\begin{aligned} \bar{w}_{j,m}(t) &= \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{+\pi} e^{i(j\tau)} v_m(t, \tau) d\tau \\ &= \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{+\pi} e^{i(j\tau)} (e^{Bt}v(0, \tau))_m d\tau, \end{aligned}$$

and hence,

$$w_{j,m}(t) \leq \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{+\pi} e^{i(j\tau)} (e^{Bt}v(0, \tau))_m d\tau, \quad 1 \leq m \leq r.$$

It is easy to see that for any $\epsilon > 0$, and $t_0 > 0$, there exist $\delta > 0$ and an integer $N > 0$ such that $w_{0,m}(t) \leq \epsilon, \forall t \in [0, t_0], 1 \leq m \leq r$, whenever $w_{j,m}(0) < \delta$ for

$-N \leq j \leq N, 1 \leq m \leq r$. Thus, $\|w_0(t)\| \leq \epsilon, \forall t \in [0, t_0]$, whenever $\|w_j(0)\| < \delta$ for $-N \leq j \leq N$. Regarding the case that $y(0) \not\leq \tilde{y}(0)$, let $\tilde{z}(t), z(t)$ be two solutions of (4.4.18) with

$$\tilde{z}_{j,m}(0) = \max\{y_{j,m}(0), \tilde{y}_{j,m}(0)\}, z_{j,m}(0) = \min\{y_{j,m}(0), \tilde{y}_{j,m}(0)\}$$

for all $j \in \mathbb{Z}, 1 \leq m \leq r$. Since $z(0) \leq \tilde{z}(0)$, we have $\|y_0(t) - \tilde{y}_0(t)\| \leq \|\tilde{z}_0(t) - z_0(t)\| < \epsilon, \forall t \in [0, t_0]$, whenever $\|y_j(0) - \tilde{y}_j(0)\| = \|\tilde{z}_j(0) - z_j(0)\| < \delta, \forall j \in \mathbb{Z}$. This proves the claim.

Claim 2. For any $t_0 > 0$, $Q_t(u)$ is continuous in u uniformly for $t \in [0, t_0]$.

Fix \bar{u} and $t_0 > 0$. $\forall \epsilon > 0$. By Claim 1, it follows that for any $\epsilon > 0$, there are δ and N such that

$$\|y_{j_0}(t, u) - y_{j_0}(t, \bar{u})\| < \frac{1}{4}\epsilon, \forall t \in [0, t_0]. \quad (4.4.28)$$

whenever $\|u_j - \bar{u}_j\| < \delta, \forall j_0 \in \mathbb{Z}, \forall j_0 - N \leq j \leq j_0 + N$.

Choose $b > 0$ such that $\sum_{k=b+1}^{\infty} \frac{\|v^*\|}{2^k} < \frac{\epsilon}{4}$, and let $\delta_1 = 2^{-(b+N)}\delta$. Thus, for any $u \in \mathbb{C}_v^*$ with

$$d(u, \bar{u}) = \sum_{k=0}^{\infty} \frac{\max_{-k \leq j \leq k} \|u_j - \bar{u}_j\|}{2^k} < \delta_1,$$

we have

$$\max_{|j| \leq b+N} \|u_j - \bar{u}_j\| < 2^{b+N}\delta_1 := \delta.$$

By (4.4.28), it follows that

$$\|y_{j_0}(t, u) - y_{j_0}(t, \bar{u})\| < \frac{1}{4}\epsilon, \forall t \in [0, t_0], \forall j_0 \in [-b, b],$$

and hence,

$$\begin{aligned} d(y(t, u), y(t, \bar{u})) &\leq \max_{-b \leq j \leq b} \|y_j(t, u) - y_j(t, \bar{u})\| \sum_{k=0}^b \frac{1}{2^k} + \sum_{k=b+1}^{\infty} \frac{2\|v^*\|}{2^k} \\ &< \frac{\epsilon}{4} \sum_{k=0}^{\infty} \frac{1}{2^k} + \frac{\epsilon}{2} = \epsilon, \end{aligned}$$

whenever $d(u, \bar{u}) < \delta_1$. This proves Claim 2.

By Claim 2, it easily follows that $Q_t(u) = Q(t, u)$ is continuous in $(t, u) \in \mathbb{R} \times \mathbb{C}_{v^*}$ with respect to the compact open topology.

Note that system (4.4.26) has two equilibria 0 and v^* , and v^* is the unique globally asymptotically stable equilibrium in $[0, 1]^r \setminus \{0\}$. Since (4.4.26) is cooperative and irreducible, Theorem 1.2.1 implies that there exists an entire strongly monotone orbit such that $\lim_{t \rightarrow -\infty} v(t) = 0$ and $\lim_{t \rightarrow \infty} v(t) = v^*$. Thus, (A5) is satisfied.

By an argument similar to that in the proof of Proposition 4.3.1, we can prove that for each $t > 0$, Q_t is subhomogeneous on \mathbb{C}_{v^*} . ■

Let c^* be the spreading speed of the map Q_1 . In order to compute c^* , we consider the linearized equation (4.4.18) at $y = 0$,

$$\begin{aligned} \frac{dy_{j,m}(t)}{dt} &= \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} y_{j-k,n}(t) p_{mn}(k) - \mu_m y_{j,m}(t), \\ j &\in \mathbb{Z}, \quad 1 \leq m \leq r. \end{aligned} \tag{4.4.29}$$

Let $\{M_t\}_{t \geq 0}$ be the solution semiflow associated with the system (4.4.29). Note that $Q_t(y^0)$ is a lower solution of linear system (4.4.29) for $t \in [0, \infty)$. It then follows that

$$Q_t(y^0) \leq M_t(y^0), \quad \forall y^0 \in \mathbb{C}_{v^*}, \forall t \geq 0.$$

For each $u^0 \in \mathbb{R}^r$, let $\eta_m(t, u^0)$ be the unique solution of the linear equation

$$\frac{d\eta_m(t)}{dt} = \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} e^{\chi k} \eta_n(t) p_{mn}(k) - \mu_m \eta_m(t), \quad 1 \leq m \leq r, \quad (4.4.30)$$

with $\eta(0, u^0) = u^0$. Then we have

$$\frac{d\eta(t)}{dt} = C(\chi)\eta, \quad (4.4.31)$$

where

$$C(\chi) = \begin{pmatrix} -\mu_1 + \zeta_{11} & \zeta_{12} & \cdots & \zeta_{1r} \\ \vdots & \vdots & \ddots & \vdots \\ \zeta_{r1} & \zeta_{r2} & \cdots & -\mu_r + \zeta_{rr} \end{pmatrix},$$

with $\zeta_{ij} = \alpha_{ij} \sum_{k=-\infty}^{\infty} e^{\chi k} p_{ij}(k)$. It is easy to see that $y_j(t) = \{y_{j,m}(t)\}_{1 \leq m \leq r}$ with $y_{j,m}(t) = e^{-\chi j} \eta_m(t, u^0)$ is a solution of (4.4.29). Thus we have

$$B_\chi^t(u^0) := M_t(e^{-\chi j} u^0)(0) = \eta(t, u^0),$$

which implies that B_χ^t is the solution map of (4.4.31). Note that the general solution of (4.4.31) is $\eta(t, u^0) = e^{Ct} u^0$. Then $B_\chi^t(u^0) = e^{Ct} u^0$, and $e^{\mu(C)t}$ is the principal eigenvalue of B_χ^t with the positive eigenfunction u^0 , where $\mu(C)$ is the principle eigenvalue of the matrix C . When $\chi = 0$, we have the principal eigenvalue $e^{\mu(C)t} > 1$. Thus the map M_t satisfies the assumptions (B1)-(B7) for each $t > 0$.

Let $t = 1$. Then $\lambda(\chi) := e^{\mu(C)}$ is the principal eigenvalue of B_χ^1 . Define the function

$$\Phi(\chi) := \frac{1}{\chi} \ln \lambda(\chi) = \frac{\mu(C)}{\chi}.$$

Next we prove that $\lim_{\chi \rightarrow \infty} \Phi(\chi) = \infty$. First, we denote $C := (c_{ij})_{r \times r}$. Since C is cooperative and irreducible, $\mu(C)$ is a simple eigenvalue of C with a strongly positive eigenvector. Let $v = v(\chi)$ be the strongly positive eigenvector of C associated with the eigenvalue $\mu(C)$ such that $\|v\| = 1$. Then $Cv = \mu(C)v$. Since

$$\sum_{k=-\infty}^{\infty} e^{\chi k} p_{ij}(k) > \sum_{k=1}^{\infty} e^{\chi k} p_{ij}(k) > e^{\chi} \sum_{k=1}^{\infty} p_{ij}(k) > 0,$$

we have $\lim_{\chi \rightarrow \infty} \frac{\sum_{k=-\infty}^{\infty} e^{\chi k} p_{ij}(k)}{\chi} = \infty$, and hence, $\lim_{\chi \rightarrow \infty} \frac{c_{ij}(\chi)}{\chi} = \infty$ for all $1 \leq i, j \leq r$ with $\alpha_{ij} > 0$. By [34, Lemma 3.8], $L = \lim_{\chi \rightarrow \infty} \frac{\mu(C)}{\chi}$ exists, and it is either a finite real number or infinite. Assume, by contradiction, that L is finite. By the compactness of the sphere $\{v \in \mathbb{R}^r : \|v\| = 1\}$, there is a sequence of numbers χ_h satisfying $\lim_{h \rightarrow \infty} \chi_h = \infty$ and a vector $w = (w_i)_{i=1}^r \geq 0$ in \mathbb{R}^r with $\|w\| = 1$ such that $\lim_{h \rightarrow \infty} v(\chi_h) = w$. By the irreducibility of the matrix Λ , for any $1 \leq j \leq r$, there is $\alpha_{ij} > 0$ for some $i \neq j$.

Thus,

$$\sum_{m=1}^r \frac{c_{im}(\chi_h)}{\chi_h} v_m(\chi_h) = \frac{\mu(C(\chi_h))}{\chi_h} v_i(\chi_h), \forall h \geq 1.$$

Letting $h \rightarrow \infty$ in the above equality, we obtain that $w_j = 0, \forall 1 \leq j \leq r$, and hence, $w = 0$, which is a contradiction. Thus, $\lim_{\chi \rightarrow \infty} \Phi(\chi) = \infty$.

Since $\lim_{\chi \rightarrow 0} \Phi(\chi) = \infty$ and $\lim_{\chi \rightarrow \infty} \Phi(\chi) = \infty$, $\Phi(\chi)$ assumes its minimum at some finite value χ^* . Since $Q_1(y^0) \leq M_1(y^0), \forall y^0 \in \mathbb{C}_{v^*}$, Theorem 1.3.1 implies that

$$c^* \leq \inf_{\chi > 0} \Phi(\chi).$$

Consider the linear system

$$\frac{dy_{j,m}(t)}{dt} = (1 - \epsilon) \sum_{k=-\infty}^{\infty} \sum_{n=1}^r \alpha_{mn} y_{j-k,n}(t) p_{mn}(k) - \mu_m y_{j,m}(t), \quad (4.4.32)$$

with parameter ϵ . Let $\{M_t^\epsilon\}_{t \geq 0}$ be the solution semiflow associated with the system (4.4.32). For any $0 < \epsilon < 1$, there is a $0 < \delta < \epsilon$ such that $0 \leq y_{j,m}(t) \leq v_m(t, \bar{\delta}) < \epsilon, \forall j \in \mathbb{Z}, 1 \leq m \leq r, \forall t \in [0, 1]$ provided $0 \leq y_{j,m}(0) < \delta, \forall j \in \mathbb{Z}, 1 \leq m \leq r$, where $v(t, \bar{\delta}) = (v_1(t, \bar{\delta}), \dots, v_r(t, \bar{\delta}))$ is the solution of (4.4.26) satisfying $v(0, \bar{\delta}) = \bar{\delta} := (\delta, \dots, \delta) \in \mathbb{R}^r$. Thus, $Q_t(y^0)$ is an upper solution of linear system (4.4.32) for $t \in [0, 1]$. It then follows that $Q_t(y^0) \geq M_t^\epsilon(y^0), \forall t \in [0, 1], \forall y^0 \in \mathbb{C}_{\bar{\delta}}$. In particular, we have $Q_1(y^0) \geq M_1^\epsilon(y^0)$. As we did for $\{M_t\}_{t \geq 0}$, a similar analysis can be made for $\{M_t^\epsilon\}_{t \geq 0}$. By Theorem 1.3.1, we then have that

$$\inf_{\chi > 0} \Phi_\epsilon(\chi) \leq c^* \leq \inf_{\chi > 0} \Phi(\chi), \quad \forall \epsilon \in (0, 1).$$

Letting $\epsilon \rightarrow 0$, we obtain

$$c^* = \inf_{\chi > 0} \Phi(\chi) = \Phi(\chi^*).$$

As the consequences of Theorem 1.3.2 and Theorem 4.4.2, and Theorem 1.3.3, respectively, we have the following two results.

Theorem 4.4.3 *Assume that (D1) and (D3) hold. Let $y(t)$ be a solution of (4.4.18) with $y(0) \in \mathbb{C}_{v^*}$. Then the following statements are valid:*

(1) *For any $c > c^*$, if $y(0) \ll v^*$ and $y_j(0) = 0$ for j outside a bounded interval, then*

$$\lim_{t \rightarrow \infty, |j| \geq ct} y_j(t) = 0.$$

- (2) For any $c \in (0, c^*)$, there is an $r > 0$ such that if $y_j(0) > 0$ for j on an interval of length $2r$, then $\lim_{t \rightarrow \infty, |j| \leq ct} y_j(t) = v^*$.
- (3) If, in addition, (D2) holds, then $y(0) \neq 0$ implies that $\lim_{t \rightarrow \infty, |j| \leq ct} y_j(t) = v^*$ for any $c \in (0, c^*)$.

Theorem 4.4.4 Assume that (D1) and (D3) hold. The following two statements are valid:

- (1) For any $c \in (0, c^*)$, system (4.4.18) has no traveling wave $U(j - ct)$ connecting v^* to 0;
- (2) For any $c > c^*$, system (4.4.18) has a traveling wave $U(j - ct)$ connecting v^* to 0 such that $U(s)$ is continuous and non-increasing in $s \in \mathbb{R}$.

Numerical Simulations. To show our results on the spreading speed and traveling wave solutions, we numerically simulate system (4.2.2). Assume that $\sigma\lambda = 0.5, \mu = 0.2, p(k) = \frac{1}{3 \times 2^k}, \forall k \in \mathbb{Z}$. Then we have $v^* = 0.6$. By Theorem 4.3.1, it follows that for any initial value with compact support, the corresponding solution of (4.2.2) satisfies

$$\lim_{t \rightarrow \infty, |j| \geq ct} y_j(t) = 0, \forall c > c^*,$$

$$\lim_{t \rightarrow \infty, |j| \leq ct} y_j(t) = v^*, \forall c \in (0, c^*).$$

Let $y_0(0) = 0.3, y_j(0) = 0, \forall j \neq 0$. Figure 4.1 illustrates the numerical solution. Here the z -axis represents the value of $y_j(t)$ corresponding to the j on the x -axis and time

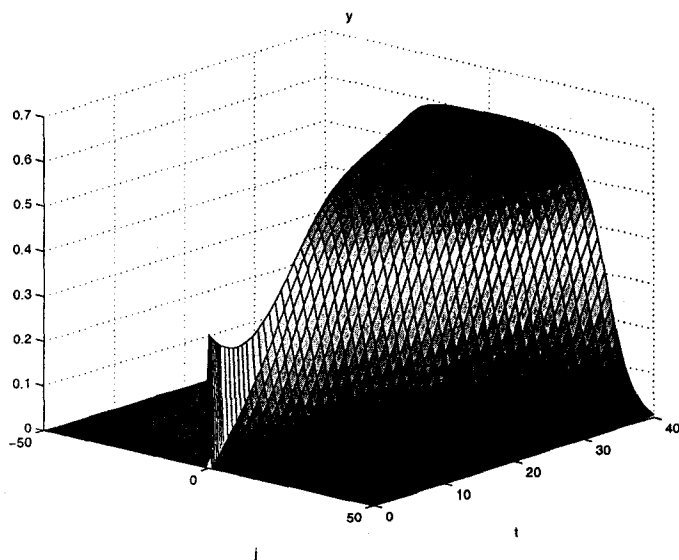


Figure 4.1: The solution of system (4.2.2): A solution with compact support.

t on the y -axis. The result is consistent with the above two properties. On the other hand, Figure 4.2 shows the numerical solution, which converges quickly to a traveling wave, with the initial value $y_j(0) = 0, \forall j \in [-N, -1], y_0(0) = 0, y_j(0) = 0.6, \forall j \in [1, N]$.

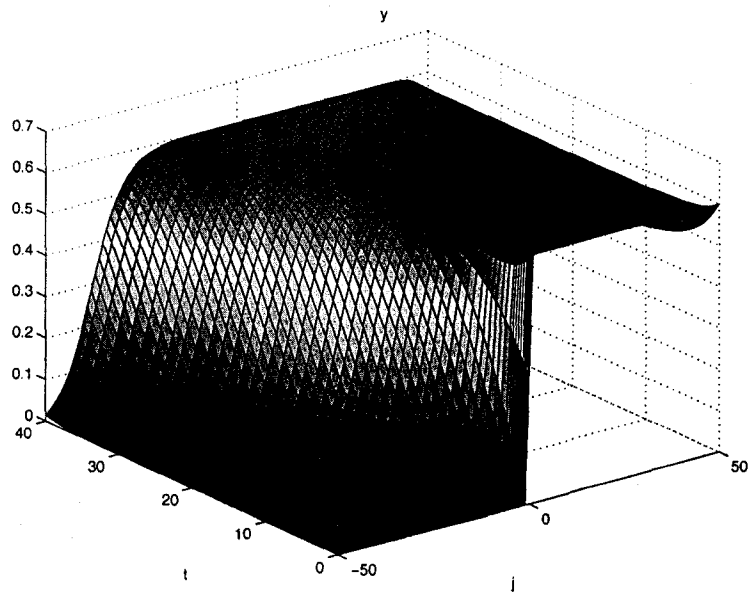


Figure 4.2: The solution of system (4.2.2): A traveling wave solution.

Chapter 5

A Reaction-Diffusion Model With a Quiescent Stage

This chapter is devoted to the investigation of the asymptotic behavior for a reaction-diffusion model with a quiescent stage. We first establish the existence of asymptotic speed of spread and show that it coincides with the minimal wave speed for monotone traveling waves. Then we obtain a threshold result on the global attractivity of either zero or positive steady state in the case where the spatial domain is bounded. The numerical simulations are also provided to illustrate these analytic results.

This chapter is organized as follows. In Section 5.1, we present the model. In Section 5.2, we study the model (5.1.3) with spatial domain being \mathbb{R} . By the theory of spreading speeds and traveling waves for monotone semiflows (see, [34], [33]), we establish the existence of asymptotic spreading speed and show that it coincides with the minimal wave speed for monotone traveling waves. In Section 5.3, by appealing to the theory of monotone dynamical systems, we investigate the global dynamics of the model (5.1.3) in a bounded domain $\Omega \subset \mathbb{R}^n$. In Section 5.4, we provide some numerical simulation results. At last, we discuss the critical domain size in Section

5.5.

5.1 Introduction

It is well known that the nonlinear reaction diffusion equation

$$\partial_t u(t, x) = D\Delta u(t, x) + f(u) \quad (5.1.1)$$

can be used to describe the dispersal dynamics of a population, where $D > 0$ denotes the diffusion coefficient, $f(u)$ is a nonlinear continuous function. To consider the individual variability, Lewis and Schemitz [31] studied the following model for a population with the individuals switch between mobile and stationary states during their lifetime,

$$\begin{cases} \partial_t u_1(t, x) = D\Delta u_1(t, x) - \mu u_1(t, x) - \gamma_2 u_1(t, x) + \gamma_1 u_2(t, x), \\ \partial_t u_2(t, x) = r u_2(t, x)(1 - u_2(t, x)/K) - \gamma_1 u_2(t, x) + \gamma_2 u_1(t, x), \end{cases} \quad (5.1.2)$$

where u_1 , u_2 are the densities of the dispersal and nondispersal subpopulations, γ_1 and γ_2 are the emigration and immigration rates, respectively, and μ is the mortality rate. The sedentary subpopulation reproduces with the intrinsic growth rate r and is subject to a finite carrying capacity K . All of the parameters in this model are positive constants. The authors of [31] determined the minimal wave speed for monotone traveling waves under the assumption that the emigration rate γ_1 is less than the intrinsic growth rate r for the sedentary class.

Hadeler and Lewis [18] studied the spreading speed for (5.1.2) by the theory presented in [54]. Since the solution map associated with (5.1.2) is not compact due to the absence of diffusion in one equation, one can not obtain the existence of monotone traveling waves by the results in [32]. Recently, Wang and Zhao [50] studied the spreading speed and traveling waves of system (5.1.2) by the theory developed in [47] for nonlinear integral equations, and they proved that the spreading speed is indeed the minimal wave speed for monotone traveling waves.

In [18], Hadeler and Lewis also presented and discussed briefly the following model

$$\begin{cases} \partial_t u_1(t, x) = D\Delta u_1(t, x) + f(u_1(t, x)) - \gamma_2 u_1(t, x) + \gamma_1 u_2(t, x), \\ \partial_t u_2(t, x) = \gamma_2 u_1(t, x) - \gamma_1 u_2(t, x), \end{cases} \quad (5.1.3)$$

which describes the dynamics of the population where the migrants reproduce, disperse at a random pace, and have a positive mortality. Such behavior is typical for invertebrates living in small ponds in arid climates which dry up and reappear subject to rainfall [18]. However, the authors of [18] did not provide further mathematical analysis.

The purpose of this chapter is to study the spatial dynamics of the system (5.1.3).

5.2 Spreading speed and traveling waves

Let \mathbb{X} be the set of all bounded and continuous functions from \mathbb{R} to \mathbb{R}^2 . Clearly, any vector in \mathbb{R}^2 can be regarded as a function in \mathbb{X} .

For $u = (u_1, u_2), v = (v_1, v_2) \in \mathbb{X}$, we write $u \geq v$ ($u \gg v$) provided $u_j(x) \geq v_j(x)$ ($u_j(x) > v_j(x)$), $\forall j = 1, 2, x \in \mathbb{R}$, and $u > v$ provided $u \geq v$ but $u \neq v$. For $r \gg 0$ in \mathbb{R}^2 , we define

$$\mathbb{X}_r := \{u \in \mathbb{X} : 0 \leq u \leq r\}.$$

Let

$$\mathbb{X}_+ := \{(u_1, u_2) \in \mathbb{X} : u_i(x) \geq 0, \forall x \in \mathbb{R}, i = 1, 2\}.$$

Then \mathbb{X}_+ is a positive cone of \mathbb{X} . We equip \mathbb{X} with the compact open topology, that is, $u^m \rightarrow u$ in \mathbb{X} means that the sequence of $u^m(x)$ converges to $u(x)$ as $m \rightarrow \infty$ uniformly for x in any compact set. Moreover, we define

$$\|u\| := \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k} |u(x)|}{2^k}, \quad \forall u \in \mathbb{X},$$

where $|\cdot|$ denotes the usual norm in \mathbb{R}^2 . It then follows that $(\mathbb{X}, \|\cdot\|)$ is a normed space, and (\mathbb{X}_r, d) is a complete metric space with the distance $d(\cdot, \cdot)$ induced by the norm $\|\cdot\|$ (see the definition on page 10). Let \mathbb{Y} be the set of all bounded and continuous functions from \mathbb{R} to \mathbb{R} , with the norm defined in a way similar to that for \mathbb{X} .

In this section, we consider the model system (5.1.3) with the spatial domain being \mathbb{R} . We assume that function $f \in C^1(\mathbb{R}_+, \mathbb{R})$ satisfies

$$(C1) \quad f(0) = 0, f'(0) > 0, \frac{d}{dv}\left(\frac{f(v)}{v}\right) < 0 \text{ for } v > 0.$$

$$(C2) \quad \text{There exists } K > 0 \text{ such that } f(v) \leq 0 \text{ for all } v \geq K.$$

We first study the reaction system associated with (5.1.3)

$$\frac{d\nu}{dt} = F(\nu), \quad (5.2.4)$$

where $\nu := \begin{pmatrix} \nu_1 \\ \nu_2 \end{pmatrix}$, and $F(\nu) := \begin{pmatrix} f(\nu_1) - \gamma_2\nu_1 + \gamma_1\nu_2 \\ \gamma_2\nu_1 - \gamma_1\nu_2 \end{pmatrix}$. By assumption (C1), we see that f is strictly subhomogeneous in the sense that $f(k\nu_1) > kf(\nu_1)$, $\forall \nu_1 > 0, k \in (0, 1)$. It then follows that the solution map associated with system (5.2.4) is strictly subhomogeneous. It is easy to see that the system is cooperative and irreducible. Thus, the solution map is strongly monotone (see, e.g., [43, Theorem 4.1.1]). Note that

$$DF(0) = \begin{pmatrix} f'(0) - \gamma_2 & \gamma_1 \\ \gamma_2 & -\gamma_1 \end{pmatrix}.$$

Let $r(DF(0))$ be the spectral radius of $DF(0)$. We then have

$$r(DF(0)) = \frac{1}{2} \left(f'(0) - \gamma_1 - \gamma_2 + \sqrt{(f'(0) - \gamma_1 - \gamma_2)^2 + 4f'(0)\gamma_1} \right) > 0.$$

By the assumptions (C1) and (C2), there exists $u_1^* > 0$ such that $f(u_1^*) = 0$ and $f(\nu_1) \leq 0, \forall \nu_1 > u_1^*$. Define $u_2^* := \frac{\gamma_2 u_1^*}{\gamma_1}$. Then $w^* := (u_1^*, u_2^*)$ is an equilibrium of (5.2.4). The assumption (C2) also implies that $[0, \bar{w}]$ with $\bar{w} = (\bar{w}_1, \frac{\gamma_2 \bar{w}_1}{\gamma_1})$ is positively invariant for any $\bar{w}_1 \geq u_1^*$. By the continuous-time version of [63, Theorem 2.3.4] and [63, Lemma 2.2.1], we have the following result.

Lemma 5.2.1 *Assume that (C1) and (C2) hold. Then $w^* = (u_1^*, u_2^*)$ is globally asymptotically stable for (5.2.4) in $\mathbb{R}^2 \setminus \{0\}$.*

Let $\Gamma(t, x)$ be the Green's function associated with the heat equation $\partial_t u_1 = D\Delta u_1$. Then $\partial_t u_1 = D\Delta u_1 - \gamma_2 u_1$ generates a linear C^0 -semigroup $T_1(t)$, which is defined by

$$(T_1(t)\phi_1)(x) := e^{-\gamma_2 t} \int_{\mathbb{R}} \Gamma(t, x-y) \phi_1(y) dy. \quad (5.2.5)$$

Let $b > 0$ and $t > 0$ be given. For any $\epsilon > 0$ and $K > 0$, there exists $M > 0$, such that $\int_{|y| \geq M} \Gamma(t, y) dy < e^{\gamma_2 t} \epsilon / 4b$. Let $\delta = e^{\gamma_2 t} \epsilon / 2$, $L = M + K$. Then for any $\phi_1, \psi_1 \in [-b, b]_{\mathbb{Y}}$, we have

$$\begin{aligned} |T_1(t)(\phi_1)(x) - T_1(t)(\psi_1)(x)| &= e^{-\gamma_2 t} \left| \int_{\mathbb{R}} \Gamma(t, x-y) (\phi_1(y) - \psi_1(y)) dy \right| \\ &\leq e^{-\gamma_2 t} \int_{\mathbb{R}} \Gamma(t, y) |\phi_1(x-y) - \psi_1(x-y)| dy \\ &= e^{-\gamma_2 t} \left[\int_{y \in [-M, M]} \Gamma(t, y) |\phi_1(x-y) - \psi_1(x-y)| dy \right. \\ &\quad \left. + \int_{|y| \geq M} \Gamma(t, y) |\phi_1(x-y) - \psi_1(x-y)| dy \right] \\ &\leq e^{-\gamma_2 t} \left[\max_{y \in [-M, M]} |\phi_1(x-y) - \psi_1(x-y)| \right. \\ &\quad \left. + 2b \int_{|y| \geq M} \Gamma(t, y) dy \right] \\ &< \epsilon \end{aligned}$$

for all $x \in [-K, K]$, whenever $|\phi_1(x) - \psi_1(x)| < \delta$ for $-L \leq x \leq L$. Thus, for any $b > 0$, $T_1(t) : [-b, b]_{\mathbb{Y}} \rightarrow \mathbb{Y}$ is continuous.

We consider system (5.1.3) with initial conditions

$$u_1(0, x) = \phi_1(x) \geq 0, u_2(0, x) = \phi_2(x) \geq 0, \forall x \in \mathbb{R}. \quad (5.2.6)$$

Integrating the first equation of the system (5.1.3) together with (5.2.6), we have

$$u_1(t, \cdot, \phi) = T_1(t)\phi_1 + \int_0^t T_1(t-s)(f(u_1(s)) + \gamma_1 u_2(s))ds \quad (5.2.7)$$

Note that $\partial_t u_2 = -\gamma_1 u_2$ generates a linear C^0 - semigroup $T_2(t)$, which is defined by

$$(T_2(t)\phi_2)(x) := e^{-\gamma_1 t}\phi_2(x),$$

and

$$\begin{aligned} \|T_2(t)(\phi_2) - T_2(t)(\psi_2)\| &= e^{-\gamma_1 t} \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k} |\phi_2(x) - \psi_2(x)|}{2^k} \\ &= e^{-\gamma_1 t} \|\phi_2 - \psi_2\|. \end{aligned}$$

It is easy to see that the linear operator $T_2(t)$ is continuous with respect to the norm in \mathbb{X} for each $t \geq 0$.

Integrating the second equation of system (5.1.3) together with (5.2.6), we obtain

$$u_2(t, \cdot, \phi) = T_2(t)\phi_2 + \gamma_2 \int_0^t T_2(t-s)u_1(s)ds. \quad (5.2.8)$$

$$\text{Let } T(t) = \begin{pmatrix} T_1(t) & 0 \\ 0 & T_2(t) \end{pmatrix}, B(\phi)(x) = \begin{pmatrix} B_1(\phi)(x) \\ B_2(\phi)(x) \end{pmatrix} = \begin{pmatrix} f(\phi_1)(x) + \gamma_1 \phi_2(x) \\ \gamma_2 \phi_1(x) \end{pmatrix}.$$

Clearly, $T(t)$ is a linear semigroup on \mathbb{X} .

It follows that system (5.1.3) can be written as the following integral equation:

$$u(t) = T(t)\phi + \int_0^t T(t-s)B(u(s))ds. \quad (5.2.9)$$

A function $\hat{u}(t, x)$ is said to be a lower solution of (5.1.3) if

$$\hat{u}(t) \leq T(t)\phi + \int_0^t T(t-s)B(\hat{u}(s))ds, \forall t \geq 0.$$

A function $\bar{u}(t, x)$ is said to be an upper solution of (5.1.3) if

$$\bar{u}(t) \geq T(t)\psi + \int_0^t T(t-s)B(\bar{u}(s))ds, \forall t \geq 0.$$

Lemma 5.2.2 *Let (C1) and (C2) hold. For any $\phi = (\phi_1, \phi_2) \in \mathbb{X}_{w^*}$, the system (5.1.3) has a unique mild solution $u(t, x, \phi) = (u_1(t, x, \phi), u_2(t, x, \phi))$ with $u(0, \cdot, \phi) = \phi$, and $u(t, \cdot, \phi) \in \mathbb{X}_{w^*}, \forall t \geq 0$. Moreover, if $\hat{u}(t, x)$ and $\bar{u}(t, x)$ are a pair of lower and upper solutions of (5.1.3), respectively, with $\hat{u}(0, \cdot) \leq \bar{u}(0, \cdot)$, then $\hat{u}(t, \cdot) \leq \bar{u}(t, \cdot), \forall t \geq 0$.*

Proof. We first show that B is quasi-monotone on \mathbb{X}_{w^*} in the sense that

$$\lim_{h \rightarrow 0+} \frac{1}{h} d(\psi - \phi + h(B(\psi) - B(\phi)); \mathbb{X}_+) = 0$$

for all $\phi, \psi \in \mathbb{X}_{w^*}$ with $\phi(x) \leq \psi(x), x \in \mathbb{R}$. Indeed, it is easy to see that there is a constant $\rho > 0$ such that

$$B(\psi) - B(\phi) = \begin{pmatrix} f(\psi_1) + \gamma_1 \psi_2 - f(\phi_1) - \gamma_1 \phi_2 \\ \gamma_2 \psi_1 - \gamma_2 \phi_1 \end{pmatrix} \geq \begin{pmatrix} -\rho(\psi_1 - \phi_1) + \gamma_1(\psi_2 - \phi_2) \\ \gamma_2(\psi_1 - \phi_1) \end{pmatrix},$$

and hence for any $h > 0$ satisfying $h\rho < 1$,

$$\psi - \phi + h(B(\psi) - B(\phi)) \geq \begin{pmatrix} (1 - h\rho)(\psi_1 - \phi_1) + h\gamma_1(\psi_2 - \phi_2) \\ (h\gamma_2 + 1)(\psi_1 - \phi_1) \end{pmatrix} \geq 0 \text{ in } \mathbb{X}_+.$$

By [39, Corollary 5], (5.1.3) has a unique mild solution $u(t, \cdot, \phi)$ on $[0, \infty)$ for each $\phi \in \mathbb{X}_{w^*}$, and the comparison principle holds for the lower and upper solutions. ■

Define a family of operators $\{Q_t\}_{t \geq 0}$ on \mathbb{X}_{w^*} by

$$Q_t(\phi)(x) := u(x, t, \phi) = (u_1(x, t, \phi), u_2(x, t, \phi)), \forall x \in \mathbb{R}, t \geq 0. \quad (5.2.10)$$

Note that for any $(t_0, \phi_0) \in \mathbb{R}_+ \times \mathbb{X}_{w^*}$, we have

$$\|Q_t(\phi) - Q_{t_0}(\phi_0)\| \leq \|Q_t(\phi) - Q_t(\phi_0)\| + \|Q_t(\phi_0) - Q_{t_0}(\phi_0)\|. \quad (5.2.11)$$

By [38, Theorem 8.5.2], it follows that $Q_t(\phi)$ is continuous at (t_0, ϕ_0) with respect to the compact open topology. Thus, $\{Q_t\}_{t \geq 0}$ is a semiflow on \mathbb{X}_{w^*} .

Lemma 5.2.3 *$\{Q_t\}_{t \geq 0}$ is a subhomogeneous and strongly monotone semiflow on \mathbb{X}_{w^*} .*

Proof. Since f is strictly subhomogeneous, we see that $(u_1(t, x, \phi), u_2(t, x, \phi)) = u(t, x, \phi)$ satisfies

$$\begin{aligned} \partial_t(\kappa u_1) &= D\kappa \Delta u_1 + \kappa f(u_1) - \gamma_2 \kappa u_1 + \gamma_1 \kappa u_2 \\ &\leq D\kappa \Delta u_1 + f(\kappa u_1) - \gamma_2 \kappa u_1 + \gamma_1 \kappa u_2 \\ \partial_t(\kappa u_2) &\leq -\gamma_2 \kappa u_1 + \gamma_1 \kappa u_2 \end{aligned}$$

for any $0 \leq \kappa \leq 1$ and $\phi \in \mathbb{X}_{w^*}$. Thus, $\kappa u(t, \phi)$ is a lower solution of (5.1.3) with initial value $\kappa \phi$. By Lemma 5.2.2, we then have $\kappa u(t, \phi) \leq u(t, \kappa \phi)$ for $t \geq 0$, that is, $\kappa Q_t(\phi) \leq Q_t(\kappa \phi)$. Thus, Q_t is subhomogeneous.

By Lemma 5.2.2, $\{Q_t\}_{t \geq 0}$ is a monotone semiflow on \mathbb{X}_{w^*} . Next, we show that for each $t > 0$, Q_t is strongly monotone in the sense that $Q_t(\phi) \ll Q_t(\psi)$ whenever $\phi < \psi$ in X_{w^*} . Given $\phi < \psi$ in X_{w^*} , let $U(t, x) = u(t, x, \psi) - u(t, x, \phi)$. Then

$U(t, x) \geq 0, \forall t \geq 0$, and $U(0, \cdot) \not\equiv 0$. Note that the first and second component $U_1(t, x)$ and $U_2(t, x)$ satisfy

$$\begin{aligned} \partial_t U_1(t, x) &= D\Delta U_1(t, x) + f(u_1(t, x, \psi)) - f(u_1(t, x, \phi)) - \gamma_2 U_1(t, x) + \gamma_1 U_2(t, x) \\ &\geq D\Delta U_1(t, x) - \rho U_1(t, x) - \gamma_2 U_1(t, x) + \gamma_1 U_2(t, x) \end{aligned} \quad (5.2.12)$$

$$\geq D\Delta U_1(t, x) - (\rho + \gamma_2) U_1(t, x, \phi). \quad (5.2.13)$$

$$\partial_t U_2(t, x) = \gamma_2 U_1(t, x) - \gamma_1 U_2(t, x). \quad (5.2.14)$$

In the case where $U_1(0, \cdot) \not\equiv 0$, the strict positivity theorem (see e.g., [49, Theorem 5.5.4]) and the inequality (5.2.13) imply that $U_1(t, x) > 0, \forall t > 0, \forall x \in \mathbb{R}$. It follows from the equation (5.2.14) that $U_2(t, x) > 0, \forall t > 0, \forall x \in \mathbb{R}$.

In the case where $U_2(0, \cdot) \not\equiv 0$, we have, by the equation (5.2.14),

$$U_2(t, \cdot) = T_2(t)U_2(0, \cdot) + \gamma_2 \int_0^t T_2(t-s)U_1(s, \cdot)ds \not\equiv 0, \forall t \geq 0.$$

Thus, (5.2.12) implies that

$$U_1(t, \cdot) \geq T_3(t)U_1(0, \cdot) + \gamma_1 \int_0^t T_3(t-s)U_2(s, \cdot)ds \not\equiv 0, \forall t > 0,$$

where $T_3(t)$ is the linear semigroup generated by $\partial_t U_1 = D\Delta U_1 - (\rho + \gamma_2)U_1$, that is,

$$(T_3(t)\phi_1)(x) := e^{-(\rho+\gamma_2)t} \int_{\mathbb{R}} \Gamma(t, x-y)\phi_1(y)dy.$$

Hence, by [49, Theorem 1.4.5], we get $U_1(t, x) > 0, \forall t > 0, \forall x \in \mathbb{R}$. It follows from the equation (5.2.14) that $U_2(t, x) > 0, \forall t > 0, \forall x \in \mathbb{R}$.

Therefore, $u(t, x, \psi) \gg u(t, x, \phi), \forall t > 0, x \in \mathbb{R}$, which implies that $Q_t : \mathbb{X}_w \rightarrow \mathbb{X}_w$ is a strongly monotone semiflow. ■

Lemma 5.2.4 *For each $t > 0$, the map Q_t satisfies (A1) – (A6) with $r = w^*$.*

Proof. It is easy to see that assumptions (A1)–(A4) are all hold for Q_t . Let \hat{Q}_t be the restriction of Q_t to $[0, w^*]$. Then $\hat{Q}_t : [0, w^*] \rightarrow [0, w^*]$ is the solution semiflow generated by the ordinary differential system (5.2.4). By Lemma 5.2.1, w^* is globally asymptotically stable equilibrium of \hat{Q}_t in $\mathbb{R}/\{0\}$. Note that \hat{Q}_t is a strongly monotone semiflow on $[0, w^*]$. By the Dancer-Hess connecting orbit lemma (see, e.g., [63]), it follows that for each $t > 0$, the map \hat{Q}_t admits a strongly monotone full orbit connecting 0 and w^* , and hence, Q_t satisfies (A5).

Define a linear operator $S(t)\phi := (0, T_2(t)\phi_2)$, $\forall \phi \in \mathbb{X}$, and a nonlinear map

$$L(t)\phi = (u_1(t, \cdot, \phi), \gamma_2 \int_0^t T_2(t-s)u_1(s)ds), \forall \phi \in \mathbb{X}_{w^*}.$$

It is easy to see that $Q_t(\phi) = S(t)\phi + L(t)\phi$, $\forall \phi \in \mathbb{X}_{w^*}$, $t \geq 0$. Since

$$\|S(t)\phi\| = \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k} |(S(t)\phi)(x)|}{2^k} = e^{-\gamma_1 t} \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k} |(0, \phi_2(x))|}{2^k} \leq e^{-\gamma_1 t} \|\phi\|,$$

we have $\|S(t)\| \leq e^{-\gamma_1 t}$, $\forall t > 0$. By the expression of (5.2.7) and the compactness of $T_1(t) : [-b, b]_{\mathbb{Y}} \rightarrow \mathbb{Y}$ for each $t > 0$ and $b > 0$, it then follows that $L(t) : \mathbb{X}_{w^*} \rightarrow \mathbb{X}_+$ is compact for each $t > 0$. Thus, for any number $r > 0$, any interval $I = [a, b]$ of the length r , and any $\mathcal{D} \subset \mathbb{X}_{w^*}$, we have

$$\alpha((Q_t(\mathcal{D}))_I) \leq \alpha((S(t)(\mathcal{D}))_I) + \alpha((L(t)(\mathcal{D}))_I) \leq e^{-\gamma_1 t} \alpha(\mathcal{D}_I),$$

which implies that (A6) is satisfied. ■

Let c^* be the asymptotic speed of spread of the map Q_1 on \mathbb{X}_{w^*} . In order to compute c^* , we consider the linear differential equation

$$\begin{cases} \frac{d\bar{u}_1(t)}{dt} = D\mu^2\bar{u}_1(t) + f'(0)\bar{u}_1(t) - \gamma_2\bar{u}_1(t) + \gamma_1\bar{u}_2(t), \\ \frac{d\bar{u}_2(t)}{dt} = \gamma_2\bar{u}_1(t) - \gamma_1\bar{u}_2(t). \end{cases} \quad (5.2.15)$$

Let $(\bar{u}_1(t, w), \bar{u}_2(t, w))$ be the solution of (5.2.15) satisfying $(\bar{u}_1(0, w), \bar{u}_2(0, w)) = w \in \mathbb{R}^2$.

It is easy to see that $(u_1(t, x), u_2(t, x)) = e^{-\mu x}(\bar{u}_1(t, w), \bar{u}_2(t, w))$ is the solution of the linear differential equation with diffusion

$$\begin{cases} \partial_t u_1(t, x) = D\Delta u_1(t, x) + f'(0)u_1(t, x) - \gamma_2 u_1(t, x) + \gamma_1 u_2(t, x), \\ \partial_t u_2(t, x) = \gamma_2 u_1(t, x) - \gamma_1 u_2(t, x). \end{cases} \quad (5.2.16)$$

Let $\{M_t\}_{t \geq 0}$ be the solution semiflow associated with the system (5.2.16). Note that $Q_t(\phi)$ is a lower solution of the linear system (5.2.16) for $t \in [0, \infty)$. It then follows that

$$Q_t(\phi) \leq M_t(\phi), \forall \phi \in \mathbb{X}_{w^*}, \forall t \geq 0.$$

Note that the fundamental solution matrix of (5.2.15) is $e^{A(\mu)t}$ with

$$A(\mu) = \begin{pmatrix} D\mu^2 + f'(0) - \gamma_2 & \gamma_1 \\ \gamma_2 & -\gamma_1 \end{pmatrix}.$$

Define B_μ^t as

$$B_\mu^t(\phi) := M_t(\phi e^{-\mu x})(0) = (\bar{u}_1(t, \phi), \bar{u}_2(t, \phi)) = e^{A(\mu)t}\phi,$$

Therefore, B_μ^t is the solution map of the linear differential equations (5.2.15) on \mathbb{R}^2 , and its principal eigenvalue is $e^{\lambda(\mu)t}$, where $\lambda(\mu)$ is the spectral radius of the matrix $A(\mu)$, and

$$\lambda(\mu) = \frac{1}{2} \left[D\mu^2 + f'(0) - \gamma_2 - \gamma_1 + \sqrt{(D\mu^2 + f'(0) - \gamma_2 - \gamma_1)^2 + 4\gamma_1(D\mu^2 + f'(0))} \right].$$

Since $\lambda(0) > 0$, the map M_t satisfies assumptions (B1)-(B7) for each $t > 0$.

Letting $t = 1$, we see that $e^{\lambda(\mu)}$ is the principal eigenvalue of $B_\mu^1 =: B_\mu$. Define the function

$$\Phi(\mu) := \frac{1}{\mu} \ln e^{\lambda(\mu)} = \frac{\lambda(\mu)}{\mu}, \quad \forall \mu > 0. \quad (5.2.17)$$

Since $\lim_{\mu \rightarrow 0} \Phi(\mu) = \infty$, and $\lim_{\mu \rightarrow \infty} \Phi(\mu) = \infty$, $\Phi(\mu)$ assumes its minimum at some finite value μ^* . It then follows from Theorem 1.3.1 that $c^* \leq \inf_{\mu > 0} \Phi(\mu)$.

For any $0 < \epsilon < 1$, there is $\delta > 0$ such that $f(v) \geq (1 - \epsilon)f'(0)v, \forall 0 \leq v \leq \delta$. By the continuous dependence of solutions on initial conditions, it follows that there is a sufficient small $\eta > 0$ such that the solution of (5.2.4) satisfies $\nu(t, \bar{\eta}) < \bar{\delta}, \forall x \in \mathbb{R}, \forall t \in [0, 1]$, where $\bar{\delta} = (\delta, \delta), \bar{\eta} = (\eta, \eta)$. Thus, the comparison theorem (see Lemma 5.2.2) implies that

$$u(t, x, \phi) \leq v(t, \eta) \leq \delta, \forall x \in \mathbb{R}, \forall \phi \in \mathbb{X}_\eta, \forall t \in [0, 1].$$

Hence for all $t \in [0, 1]$ and $x \in \mathbb{R}$, $u(t, x, \phi)$ with $\phi \in \mathbb{X}_\eta$ satisfies

$$\begin{cases} \partial_t u_1(t, x) \geq D\Delta u_1(t, x) + (1 - \epsilon)f'(0)u_1(t, x) - \gamma_2 u_1(t, x) + \gamma_1 u_2(t, x), \\ \partial_t u_2(t, x) = \gamma_2 u_1(t, x) - \gamma_1 u_2(t, x). \end{cases} \quad (5.2.18)$$

Let $\{M_t^\epsilon\}_{t \geq 0}$ be the solution semiflow associated with

$$\begin{cases} \partial_t \tilde{u}_1(t, x) = D\Delta \tilde{u}_1(t, x) + (1 - \epsilon)f'(0)\tilde{u}_1(t, x) - \gamma_2 \tilde{u}_1(t, x) + \gamma_1 \tilde{u}_2(t, x), \\ \partial_t \tilde{u}_2(t, x) = \gamma_2 \tilde{u}_1(t, x) - \gamma_1 \tilde{u}_2(t, x). \end{cases} \quad (5.2.19)$$

Since $Q_t(\phi)$ is an upper solution of the linear system (5.2.19) for $t \in [0, 1]$ and $\phi \in \mathbb{X}_\eta$.

It then follows that

$$M_t^\epsilon(\phi) \leq Q_t(\phi), \forall \phi \in \mathbb{X}_\eta, \forall t \in [0, 1].$$

In particular, $M_1^\epsilon(\phi) \leq Q_1(\phi), \forall \phi \in \mathbb{X}_\eta$. As for $\{M_t\}_{t \geq 0}$, similar analysis can be carried out for $\{M_t^\epsilon\}_{t \geq 0}$. By Theorem 1.3.1, we then have

$$\inf_{\mu > 0} \Phi_\epsilon(\mu) \leq c^* \leq \inf_{\mu > 0} \Phi(\mu), \quad \forall \epsilon \in (0, 1).$$

Letting $\epsilon \rightarrow 0$, we obtain $c^* = \inf_{\mu > 0} \Phi(\mu)$. Setting $\Phi'(\mu) = 0$, we then have the following equation

$$\begin{aligned} D^3 \mu^6 + [3f'(0)D^2 - 2D^2(f'(0) - \gamma_1 - \gamma_2)]\mu^4 - D(f'(0) - \gamma_1 - \gamma_2) \cdot \\ (f'(0) + \gamma_1 + \gamma_2)\mu^2 - 4\gamma_1(f'(0))^2 - f'(0)(f'(0) - \gamma_1 - \gamma_2)^2 = 0. \end{aligned} \quad (5.2.20)$$

Thus, $c^* = \Phi(\mu^*)$, where μ^* is the positive root of (5.2.20) at which $\Phi(\mu)$ takes its minimum value.

The following result shows that the above-defined c^* is the spreading speed for solutions of (5.1.3) with initial functions having compact supports.

Theorem 5.2.5 *Assume that (C1) and (C2) hold, and let $c^* = \inf_{\mu > 0} \Phi(\mu)$. Then the following statements are valid:*

- (1) For any $c > c^*$, if $\phi \in \mathbb{X}_{w^*}$ with $0 \leq \phi \ll w^*$, and $\phi(x) = 0$ for x outside a bounded interval, then $\lim_{t \rightarrow \infty, |x| \geq ct} u(t, x, \phi) = (0, 0)$;
- (2) For any $c \in (0, c^*)$, if $\phi \in \mathbb{X}_{w^*}$ and $\phi \not\equiv 0$, then $\lim_{t \rightarrow \infty, |x| \leq ct} u(t, x, \phi) = w^*$.

Proof. Conclusion (1) is straightforward consequence of the first part of Theorem 1.3.2. Let $c < c^*$ be given. Since Q_t is subhomogeneous, r_α can be chosen to be independent of $\alpha \gg 0$. Thus, we can write r_α as r . If $\phi \in \mathbb{X}_{w^*}$ and $\phi(x) \gg 0$ for x on an interval J of length $2r$, then there exists a vector $\sigma \gg 0$ such that $\phi(x) \gg \sigma$, $\forall x \in J$, and hence, the second part of Theorem 1.3.2 implies that $\lim_{t \rightarrow \infty, |x| \leq ct} u(t, x, \phi) = (u_1^*, u_2^*)$. For any $\phi \in \mathbb{X}_{w^*}$ with $\phi(\cdot) \not\equiv 0$, it follows from the strong monotonicity of Q_t that $u(t, x, \phi) \gg 0, \forall x \in \mathbb{R}, t > 0$. Fix a $t_0 > 0$. Then $u(t_0, x, \phi) \gg 0, \forall x \in \mathbb{R}$. By taking $u(t_0, x, \phi)$ as a new initial value, we have the conclusion (2). ■

The existence and nonexistence of traveling wave solutions are straightforward consequences of Theorem 1.3.3.

Theorem 5.2.6 Assume that (C1) and (C2) hold, and let $c^* = \inf_{\mu > 0} \Phi(\mu)$. Then the following statements are valid:

- (1) System (5.1.3) admits no traveling wave solution with wave speed $c \in (0, c^*)$;
- (2) For every $c \geq c^*$, system (5.1.3) has a traveling wave solution $U(x - ct)$ connecting w^* to $(0, 0)$ such that $U(s)$ is continuous and non-increasing in $s \in \mathbb{R}$.

5.3 Dynamics in a bounded domain

In this section, we consider the model system (5.1.3) with bounded spatial domain

$$\left\{ \begin{array}{l} \partial_t u_1(t, x) = D\Delta u_1(t, x) + f(u_1(t, x)) - \gamma_2 u_1(t, x) + \gamma_1 u_2(t, x), \\ \partial_t u_2(t, x) = \gamma_2 u_1(t, x) - \gamma_1 u_2(t, x) \text{ in } (0, \infty) \times \Omega, \\ Bu_i = 0 \text{ on } (0, \infty) \times \partial\Omega, \quad i = 1, 2, \\ u_i(0, \cdot) = \phi_i, \quad i = 1, 2, \end{array} \right. \quad (5.3.22)$$

where $\Omega \subset \mathbb{R}^n (n \geq 1)$ is a bounded domain with boundary $\partial\Omega$ of class $C^{1+\theta} (0 < \theta \leq 1)$, the boundary condition is either $Bu = u$ (Dirichlet boundary condition) or $Bu = \frac{\partial u}{\partial \nu} + \alpha(x)u$ (Robin type boundary condition) for some nonnegative function $\alpha \in C^{1+\theta}(\partial\Omega, \mathbb{R})$, $\frac{\partial u}{\partial \nu}$ denotes the differentiation in the direction of outward normal n to $\partial\Omega$.

Let $\mathbb{X} = L^p(\Omega), \forall n < p < \infty$, and for $\beta \in (\frac{1}{2} + \frac{n}{2p}, 1)$, let \mathbb{X}_β be the fractional power space of \mathbb{X} with respect to $-\Delta$ and the boundary condition $Bu = 0$ (see, e.g., [20]). Then \mathbb{X}_β is an ordered Banach space with the order cone \mathbb{X}_β^+ consisting of all nonnegative functions in \mathbb{X}_β , and \mathbb{X}_β^+ has nonempty interior $\text{int}(\mathbb{X}_\beta^+)$. Moreover, $\mathbb{X}_\beta \subset C^{1+\nu}(\bar{\Omega})$ with continuous inclusion for $\nu \in [0, 2\beta - 1 - \frac{n}{p})$. Let $E = \mathbb{X}_\beta \times \mathbb{X}_\beta$ and $P = \mathbb{X}_\beta^+ \times \mathbb{X}_\beta^+$. Then (E, P) is an ordered Banach space. Denote the norm on E by $\|\cdot\|_\beta$. Thus, there exists a constant $k_\beta > 0$ such that $\|\phi\|_\infty := \max_{x \in \bar{\Omega}} \|(\phi_1(x), \phi_2(x))\| \leq k_\beta \|\phi\|_\beta, \forall \phi \in E$.

Let $\Gamma(t, x)$ be the Green function associated with the linear equation $\partial_t u_1 = D\Delta u_1$ subject to the boundary condition $Bu_1 = 0$. Then the equation $\partial_t u_1 = D\Delta u_1 - \gamma_2 u_1$ generates a linear semigroup $T_1(t)$, which is defined by

$$(T_1(t)\phi_1)(x) := e^{-\gamma_2 t} \int_{\Omega} \Gamma(t, x - y) \phi_1(y) dy. \quad (5.3.23)$$

Integrating the first equation of system (5.3.22), we have

$$u_1(t, \cdot, \phi) = T_1(t)\phi_1 + \int_0^t T_1(t-s)(f(u_1(s)) + \gamma_1 u_2(s)) ds. \quad (5.3.24)$$

Similarly, $\partial_t u_2 = -\gamma_1 u_2$ generates a linear semigroup $T_2(t)$, which is defined by

$$(T_2(t)\phi_2)(x) := e^{-\gamma_1 t} \phi_2(x).$$

Since

$$\|T_2(t)(\phi_2) - T_2(t)(\psi_2)\|_{\beta} = \|e^{-\gamma_1 t} \phi_2 - e^{-\gamma_1 t} \psi_2\|_{\beta} = e^{-\gamma_1 t} \|\phi_2 - \psi_2\|_{\beta},$$

it is easy to see that the linear operator $T_2(t)$ is continuous with respect to the norm $\|\cdot\|_{\beta}$.

Integrating the second equation of system (5.3.22), we obtain

$$u_2(t, \cdot, \phi) = T_2(t)\phi_2 + \gamma_2 \int_0^t T_2(t-s)u_1(s) ds. \quad (5.3.25)$$

$$\text{Let } T(t) = \begin{pmatrix} T_1(t) & 0 \\ 0 & T_2(t) \end{pmatrix}, B(\phi)(x) = \begin{pmatrix} B_1(\phi)(x) \\ B_2(\phi)(x) \end{pmatrix} = \begin{pmatrix} f(\phi_1)(x) + \gamma_1 \phi_2(x) \\ \gamma_2 \phi_1(x) \end{pmatrix}.$$

Clearly, $T(t)$ is a linear semigroup on E .

We write (5.3.22) as an integral equation

$$u(t) = T(t)\phi + \int_0^t T(t-s)B(u(s))ds. \quad (5.3.26)$$

For any $L > u_1^*$, let $P_L := \{\phi \in P : \phi_1(x) \leq L, \phi_2(x) \leq \frac{\gamma_2}{\gamma_1}L, \forall x \in \bar{\Omega}\}$. An argument similar to that in the last section shows that

$$\lim_{h \rightarrow 0+} \frac{1}{h} d(\psi - \phi + h(B(\psi) - B(\phi)), P) = 0$$

for all $\psi, \phi \in P_L$ with $\phi(x) \leq \psi(x), x \in \bar{\Omega}$.

By [39, Proposition 3 and Remark 2.4], (5.3.26) has a unique solution $u(t, \phi)$ on $[0, \infty)$ for each $\phi \in P_L$. Moreover, let $\hat{u}(t, x)$ and $\bar{u}(t, x)$ be a pair of lower and upper solutions of (5.1.3), respectively, with $\hat{u}(0, \cdot) \leq \bar{u}(0, \cdot)$. Then $\hat{u}(t, \cdot) \leq \bar{u}(t, \cdot), \forall t \geq 0$. In addition, P_L is a positively invariant set for (5.3.22).

Define a family of operators $\{Q_t\}_{t \geq 0}$ on P by

$$Q_t(\phi)(x) := u(x, t, \phi), \forall \phi \in P, x \in \Omega, t \geq 0. \quad (5.3.27)$$

By similar arguments as in the proof of Lemma 5.2.3, it follows that $\{Q_t\}_{t \geq 0}$ is a strongly monotone semiflow on P .

Theorem 5.3.1 *Let (C1) and (C2) hold. Then the solution semiflow $\{Q_t\}_{t \geq 0}$ admits a connected global attractor on P .*

Proof. Define a linear operator $S(t)\phi := (0, T_2(t)\phi_2), \forall \phi \in P$, and a nonlinear operator $L(t)\phi = (u_1(t, \cdot, \phi), \gamma_2 \int_0^t T_2(t-s)u_1(s)ds), \forall \phi \in P$. It is easy to see that

$Q_t(\phi) = S(t)\phi + L(t)\phi, \forall \phi \in P, t \geq 0$. Since

$$\|S(t)\phi\|_\beta = \|(0, T_2(t)\phi_2)\|_\beta = \|(0, e^{-\gamma t}\phi_2)\|_\beta \leq e^{-\gamma t} \|(\phi_1, \phi_2)\|_\beta = e^{-\gamma t} \|\phi\|_\beta,$$

we have $\|S(t)\|_\beta \leq e^{-\gamma t}, \forall t > 0$. By the expression of (5.3.24) and the compactness of $T_1(t)$ for each $t > 0$, it follows that $L(t) : P \rightarrow P$ is compact for each $t > 0$. Let α be the Kuratowski measure of noncompactness on E . Thus, for any bounded set D in P , there holds

$$\alpha(Q_t(D)) \leq \alpha(S(t)(D)) + \alpha(L(t)(D)) \leq e^{-\gamma t} \alpha(D),$$

where we have used $\alpha(L(t)(D)) = 0$ since $L(t)(D)$ is precompact. Consequently, for each $t > 0$, Q_t is an α -contraction on P with contracting function $e^{-\gamma t}$.

Next, we prove the solution semiflow Q_t is point dissipative, that is, there exists a positive number B such that

$$\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\beta \leq B, \quad \forall \phi \in P.$$

For any given $\phi \in P$, let $\nu_0 = \max_{x \in \bar{\Omega}} \phi(x)$. Denote the solution of (5.2.4) with initial value ν_0 as $\nu(t, \nu_0)$. By Lemma 5.2.1, we have $\lim_{t \rightarrow \infty} \nu(t, \nu_0) < 2w^*, \forall \nu_0 \in \mathbb{R}_+^2$. By the comparison theorem, we have $u(t, x, \phi) \leq \nu(t, \nu_0), \forall t > 0, \forall x \in \bar{\Omega}$. It follows that $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\infty < 2w^*, \forall \phi \in P$, and hence, there is $t_0 > 0$ such that $\|u(t, \cdot, \phi)\|_\infty < 2w^*, \forall t \geq t_0$. By the definition of $\|\cdot\|_0$ on $\mathbb{X}_0 = \mathbb{X}$, we have $\|u\|_0 \leq k\|u\|_\infty$ for some positive number k . It follows that $\|u(t, \cdot, \phi)\|_0 \leq k\|u(t, \cdot, \phi)\|_\infty < 2kw^*, \forall t \geq t_0$, and hence $\|u(t + t_0, \cdot, \phi)\|_0 < 2kw^*, \forall t \geq 0$. By [21, Lemma 19.3], $\|u(t + t_0, \cdot, \phi)\|_\beta \leq$

$ct^{-\gamma}\|u(t_0, \cdot, \phi)\|_0 < 2kw^*ct^{-\gamma} < 2kw^*c, \forall t \geq 1$, where $\beta < \gamma < 1$, and c depends on γ, β and kw^* . Hence, $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\beta \leq B := 2kw^*c$.

Since P_L is positively invariant for all $L > u_1^*$, the orbits of bounded sets are bounded. By the continuous-time version of [63, Theorem 1.1.2], $\{Q_t\}_{t \geq 0}$ admits a connected global attractor on P , which attracts each bounded set in P . ■

Note that $(0, 0)$ is an equilibrium of the system (5.3.22). Linearizing system (5.3.22) at $(0, 0)$, we have

$$\begin{cases} \partial_t v_1(t, x) = D\Delta v_1(t, x) + f'(0)v_1 - \gamma_2 v_1(t, x) + \gamma_1 v_2(t, x), \\ \partial_t v_2(t, x) = \gamma_2 v_1(t, x) - \gamma_1 v_2(t, x), \text{ in } \Omega \times (0, \infty), \\ Bv_i = 0, \text{ on } \partial\Omega \times (0, \infty), \quad i = 1, 2. \end{cases} \quad (5.3.28)$$

Substituting $u_i(t, x) = e^{\lambda t} \phi_i(x), i = 1, 2$, we obtain the associated eigenvalue problem

$$\begin{cases} \lambda \phi_1(x) = D\Delta \phi_1(x) + (f'(0) - \gamma_2)\phi_1(x) - \gamma_1 \phi_2(x), \\ \lambda \phi_2(x) = \gamma_2 \phi_1(x) - \gamma_1 \phi_2(x), \quad x \in \Omega, \\ B\phi_i = 0, \quad x \in \partial\Omega, \quad i = 1, 2. \end{cases} \quad (5.3.29)$$

By the proof of [43, Theorem 7.6.1] and a generalized Krein-Rutman Theorem (see, e.g., [27, Lemma 2.2]), (5.3.29) has a principal eigenvalue, denoted by λ^* , with an associated eigenvector $\phi^* = (\phi_1^*, \phi_2^*) \gg 0$.

According to [43, Theorem 7.6.1], the eigenvalue problem

$$\begin{cases} \lambda \phi_1(x) = D\Delta \phi_1(x) + (f'(0) - \gamma_2)\phi_1(x), \\ B\phi_1 = 0, \quad x \in \partial\Omega, \end{cases} \quad (5.3.30)$$

has a principal eigenvalue $\bar{\lambda}^*$ with an eigenfunction $\bar{\phi}_1^* > 0$. Moreover, we have the following observation.

Lemma 5.3.2 *The following statements are valid:*

(1) $\bar{\lambda}^* = f'(0) - \gamma_2$ in the case where $Bu = \frac{\partial u}{\partial \nu}$; and $\bar{\lambda}^* = -\frac{\pi^2 D}{L^2} + f'(0) - \gamma_2$ in the case where $Bu = u$ and $\Omega = (0, L)$.

(2) $(\bar{\lambda}^* + \gamma_1)^2 \geq 4\gamma_1\gamma_2$, and $\lambda^* = \frac{1}{2} \left[\bar{\lambda}^* - \gamma_1 + \sqrt{(\bar{\lambda}^* + \gamma_1)^2 - 4\gamma_1\gamma_2} \right]$.

Proof. In the case where $Bu = \frac{\partial u}{\partial \nu}$, it is easy to verify that $\lambda = f'(0) - \gamma_2$ is an eigenvalue of (5.3.30) with the eigenfunction $\bar{\phi}_1^* \equiv 1 \gg 0$. Since only the principal eigenvalue admits a strongly positive eigenfunction, we have $\bar{\lambda}^* = f'(0) - \gamma_2$. In the case where $Bu = u$ and $\Omega = (0, L)$, we see that $\lambda = -\frac{\pi^2 D}{L^2} + f'(0) - \gamma_2$ is an eigenvalue of (5.3.30) with the eigenfunction $\bar{\phi}_1^*(x) = \sin(\frac{\pi}{L}x)$. Since $\bar{\phi}_1^* \gg 0$ in \mathbb{X}_β , it follows that $\bar{\lambda}^* = -\frac{\pi^2 D}{L^2} + f'(0) - \gamma_2$.

Let λ^* be the principal eigenvalue of (5.3.29) with eigenfunction $\phi^* = (\phi_1^*, \phi_2^*) \gg 0$.

Then $(\lambda^* + \gamma_1)\phi_2^*(x) = \gamma_2\phi_1^*(x)$, $\forall x \in \Omega$, and hence $\lambda^* + \gamma_1 > 0$. It follows that

$$\begin{cases} (\lambda^* + \frac{\gamma_1\gamma_2}{\gamma_1 + \lambda^*})\phi_1^*(x) = D\Delta\phi_1^*(x) + (f'(0) - \gamma_2)\phi_1^*(x), \\ B\phi_1^* = 0, x \in \partial\Omega. \end{cases} \quad (5.3.31)$$

Since $\phi_1^* \gg 0$ in \mathbb{X}_β , we must have $\bar{\lambda}^* = \lambda^* + \frac{\gamma_1\gamma_2}{\gamma_1 + \lambda^*}$, and hence λ^* is a real zero of the quadratic equation

$$P(\lambda) := \lambda^2 + (\gamma_1 - \bar{\lambda}^*)\lambda + \gamma_1\gamma_2 - \gamma_1\bar{\lambda}^* = 0. \quad (5.3.32)$$

It follows that $(\bar{\lambda}^* - \gamma_1)^2 - 4(\gamma_1\gamma_2 - \bar{\lambda}^*\gamma_1) \geq 0$, which is equivalent to $(\bar{\lambda}^* + \gamma_1)^2 \geq 4\gamma_1\gamma_2$. It remains to prove that λ^* is the maximum zero of (5.3.32). Let λ be a given zero of (5.3.32). Since $P(-\gamma_1) = \gamma_1\gamma_2 > 0$, we have $\lambda \neq -\gamma_1$, i.e., $\lambda + \gamma_1 \neq 0$. It is easy to see that $\lambda(\lambda + \gamma_1) + \gamma_1\gamma_2 = \bar{\lambda}^*(\lambda + \gamma_1)$. Since $\lambda + \gamma_1 \neq 0$, we have $\bar{\lambda}^* = \lambda + \frac{\gamma_1\gamma_2}{\lambda + \gamma_1}$. Note that $\bar{\lambda}^*$ satisfies (5.3.30) with $\phi_1 = \bar{\phi}_1^*$. Set $\phi_2^* = \frac{\gamma_2}{\lambda + \gamma_1}\phi_1^*$. It then follows that λ is an eigenvalue of (5.3.29) with eigenfunction (ϕ_1^*, ϕ_2^*) . Thus, any zero of (5.3.32) is an eigenvalue of (5.3.29). Since λ^* is the principal eigenvalue of (5.3.29), it follows that λ^* is the maximum zero of (5.3.32). ■

Now we are ready to prove the following threshold result on the global dynamics of (5.3.22).

Theorem 5.3.3 *Let (C1) and (C2) hold. For any $\phi \in P$, let $u(t, \cdot, \phi)$ be the solution of (5.3.22).*

- (1) *If $\lambda^* < 0$, $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\beta = 0$ for every $\phi \in P$.*
- (2) *If $\lambda^* > 0$, then (5.3.22) admits a unique positive steady state ϕ^* , and $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi) - \phi^*\|_\beta = 0$ for every $\phi \in P \setminus \{0\}$.*

Proof. (1) In the case of $\lambda^* < 0$, [43, Theorem 7.6.2] implies that $\lim_{t \rightarrow \infty} \|v(t, \cdot, \phi)\|_\beta = 0, \forall \phi \in P$, where $v(t, \cdot, \phi)$ is the unique solution of (5.3.28). Note that the solution

$u(t, \cdot, \phi)$ of (5.3.22) satisfies

$$\begin{cases} \partial_t u_1(t, x) \leq D\Delta u_1(t, x) + f'(0)u_1 - \gamma_2 u_1(t, x) + \gamma_1 u_2(t, x), \forall t \geq 0, \\ \partial_t u_2(t, x) = \gamma_2 u_1(t, x) - \gamma_1 u_2(t, x). \end{cases} \quad (5.3.33)$$

By the comparison theorem, we have $u(t, x, \phi) \leq v(t, x, \phi)$, $\forall t \geq 0, x \in \Omega$, and hence, $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\infty = 0$. Next we show that $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\beta = 0$. Let $\omega(\phi)$ be the omega limit set of the orbit $\{u(t, \cdot, \phi) : t \geq 0\}$ with respect to the norm $\|\cdot\|_\beta$. It suffices to show that $\omega(\phi) = \{0\}$. For any $\psi \in \omega(\phi)$, there exists a sequence $t_n \rightarrow \infty$ such that $\lim_{n \rightarrow \infty} \|u(t_n, \cdot, \phi) - \psi\|_\beta = 0$, and hence, $\lim_{n \rightarrow \infty} \|u(t_n, \cdot, \phi) - \psi\|_\infty = 0$. Thus, $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\infty = 0$ implies that $\psi = 0$. It follows that $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi)\|_\beta = 0, \forall \phi \in P$.

(2) In the case of $\lambda^* > 0$, let $P_0 = \{\phi \in P : \phi(\cdot) \not\equiv 0\}$, $\partial P_0 := P \setminus P_0 = \{0\}$.

Clearly, $Q_t(0) = 0, \forall t \geq 0$. We further have the following claim.

Claim. Zero is a uniform weak repeller for P_0 in the sense that there exists $\delta_0 > 0$ such that $\limsup_{t \rightarrow \infty} \|Q_t(\phi)\|_\beta \geq \delta_0, \forall \phi \in P_0$.

Indeed, let λ_ϵ be the principal eigenvalue of

$$\begin{cases} \lambda \phi_1(x) = D\Delta \phi_1(x) + (f'(0) - \gamma_2 - \epsilon)\phi_1(x) - \gamma_1 \phi_2(x), \\ \lambda \phi_2(x) = \gamma_2 \phi_1(x) - \gamma_1 \phi_2(x), \quad x \in \Omega, \\ Bu_i = 0, \quad x \in \partial\Omega, \quad i = 1, 2 \end{cases} \quad (5.3.34)$$

with a positive eigenfunction ϕ_ϵ . Since $\lim_{\epsilon \rightarrow 0} \lambda_\epsilon = \lambda^* > 0$, we can fix a sufficiently small number $\epsilon > 0$ such that $\lambda_\epsilon > 0$. Choose $\delta_\epsilon > 0$ such that $f(u_1) > (f'(0) - \epsilon)u_1$ for all $u \in (0, \delta_\epsilon)$. Let $\delta_0 = \frac{\delta_\epsilon}{k_\beta}$. Suppose, by contradiction, there exists $\phi_0 \in P_0$ such

that $\limsup_{t \rightarrow \infty} \|Q_t(\phi_0)\|_\beta < \delta_0$, and hence, there exists $t_0 > 0$ such that $\|Q_t(\phi_0)\|_\infty \leq k_\beta \|Q_t(\phi_0)\|_\beta < \delta_\epsilon, \forall t > t_0$. It is easy to see that $u(t, x, \phi_0)$ satisfies

$$\partial_t u_1(t, x) \geq D\Delta u_1(t, x) + (f'(0) - \gamma_2 - \epsilon)u_1(t, x) + \gamma_1 u_2(t, x), x \in \Omega, \forall t \geq t_0. \quad (5.3.35)$$

Since $u_\epsilon(t, x) = \phi_\epsilon(x)e^{\lambda_\epsilon t}$ is a solution of

$$\begin{cases} \partial_t u_1(t, x) = D\Delta u_1(t, x) + (f'(0) - \gamma_2 - \epsilon)u_1(t, x) + \gamma_1 u_2(t, x), \\ \partial_t u_2(t, x) = \gamma_2 u_1(t, x) - \gamma_1 u_2(t, x), \text{ in } \Omega \times (0, \infty), \\ B_i u_i = 0, \text{ on } \partial\Omega \times (0, \infty), \end{cases} \quad (5.3.36)$$

and $u(t_0, \cdot, \phi_0) \gg 0$ in E , that is, $u(t_0, \cdot, \phi_0) \in \text{Int}(P)$, it follows that there exists a sufficiently small $a > 0$ such that $u(t_0, x, \phi_0) \geq a\phi_\epsilon(x) = au_\epsilon(0, x), \forall x \in \Omega$. By the comparison theorem, we have $u(t, x, \phi_0) \geq a\phi_\epsilon(x)e^{\lambda_\epsilon(t-t_0)}, \forall t \geq t_0, x \in \Omega$. Since $\lambda_\epsilon > 0$, it follows that $u(t, x, \phi_0)$ is unbounded, a contradiction.

By the continuous-time version of [63, Theorem 1.3.3], Q_t is uniformly persistent with respect to P_0 in the sense that there exists $\delta_1 > 0$ such that

$$\liminf_{t \rightarrow \infty} d(Q_t(\phi), \partial P_0) \geq \delta_1, \forall \phi \in P_0.$$

By the continuous-time version of [37, Theorem 3.7], the semiflow $Q_t : P_0 \rightarrow P_0, t \geq 0$, admits a global attractor A_0 . Thus, [37, Theorem 4.7] implies that $\{Q_t\}_{t \geq 0}$ has an equilibrium $\phi^* \in P_0$. Since $\{Q_t\}_{t \geq 0}$ is a strongly monotone semiflow on P , we have $\phi^* = Q_t(\phi^*) \gg 0, \forall t > 0$.

It is easy to see that for each $t > 0$, Q_t is strictly subhomogeneous. Thus, [62, Lemma 1] implies that for each $t > 0$, the map Q_t has at most one fixed point, and

hence the semiflow $\{Q_t\}_{t \geq 0}$ has at most one equilibrium. Thus, A_0 only contains one equilibrium ϕ^* . By the Hirsch attractivity theorem (see, e.g., [63, Theorem 2.2.6]), ϕ^* is globally attractive in P_0 . ■

5.4 Numerical simulations

In this section, we numerically simulate system (5.1.3) with both unbounded and bounded spatial domains.

Assume that $D = 1$, $\gamma_1 = 1$, $\gamma_2 = 1.5$, and let $f(u) = u(1-u)$. It is easy to see that (C1) and (C2) hold for system (5.1.3), and the positive equilibrium of the associated reaction system is $w^* = (1, \frac{3}{2})$. By equation (5.2.20), it follows that $\Phi(\mu)$ takes its minimum value 1.1510 at $\mu^* = 0.8074$, and hence, $c^* = \Phi(\mu^*) = 1.1510$. Thus, Theorem 5.2.5 implies that for any nonzero initial function $\phi \in \mathbb{X}_{w^*}$ with compact support, the corresponding solution of (5.1.3) satisfies

$$\begin{aligned} \lim_{t \rightarrow \infty, |x| \geq tc} u(t, x, \phi) &= 0, \quad \forall c > c^*, \\ \lim_{t \rightarrow \infty, |x| \leq tc} u(t, x, \phi) &= w^*, \quad \forall c \in (0, c^*). \end{aligned}$$

We choose

$$\phi_1(x) = \phi_2(x) = \begin{cases} 0, & \text{if } x \leq -\frac{\pi}{2}, \\ \frac{1}{2} \cos x, & \text{if } x \in [-\frac{\pi}{2}, \frac{\pi}{2}], \\ 0, & \text{if } x \geq \frac{\pi}{2}. \end{cases}$$

Figure 1 illustrates the numerical solution $u(t, x) = (u_1(t, x), u_2(t, x))$. Here we replace the spatial domain $(-\infty, \infty)$ with the large interval $[-60, 60]$ subject to the

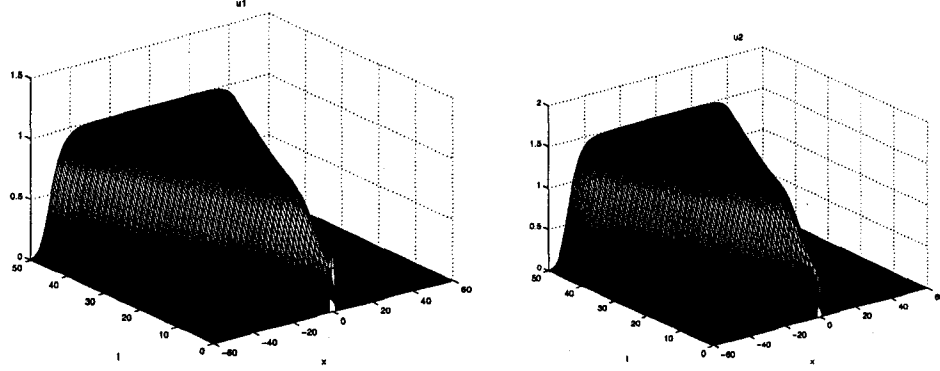


Figure 5.1: A solution with compact support

Neumann boundary condition. The result is consistent with the above two properties. To show a traveling wave, we choose the initial conditions as

$$\phi_1(x) = \begin{cases} 0, & \text{if } x \leq -1, \\ \frac{1}{2}(x+1), & \text{if } x \in [-1, 1], \\ 1, & \text{if } x \geq 1, \end{cases}$$

and

$$\phi_2(x) = \begin{cases} 0, & \text{if } x \leq -1, \\ \frac{3}{4}(x+1), & \text{if } x \in [-1, 1], \\ \frac{3}{2}, & \text{if } x \geq 1. \end{cases}$$

Figure 2 shows that the numerical solutions converge quickly to a traveling wave in profile.

Next we consider system (5.1.3) with boundary domain $\Omega = [0, \pi]$ in the case of Dirichlet boundary condition. In the case where $D = 1$, $\gamma_1 = 1$, $\gamma_2 = 1.5$, and $f(u) = u(1 - u)$, Lemma 5.3.2 implies that the eigenvalue $\lambda^* < 0$. By Theorem 5.3.3,

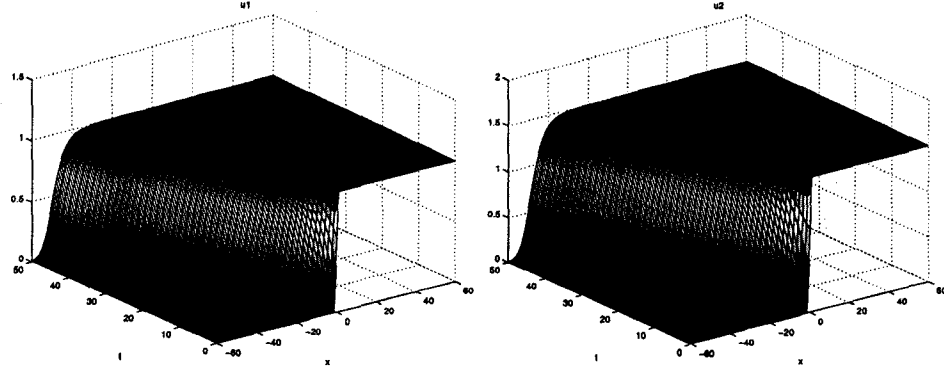


Figure 5.2: A traveling wave solution

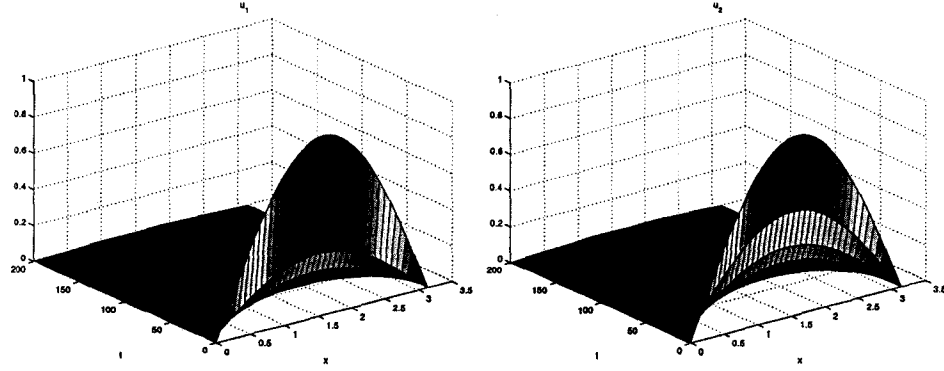


Figure 5.3: Global attractivity of the zero solution

it follows that $\lim_{t \rightarrow \infty} \|u(t, x, \phi)\|_\beta = 0$ for every $\phi \in P$. Let

$$\phi_1(x) = \phi_2(x) = \sin x, \forall x \in \Omega.$$

Figure 3 illustrates the numerical solution $(u_1(t, x), u_2(t, x))$, and confirms our result.

In the case where $D = 0.2$, $\gamma_1 = 1$, and $\gamma_2 = 0.2$, Lemma 5.3.2 implies that the eigenvalue $\lambda^* > 0$. By the second conclusion of Theorem 5.3.3, it follows that there exists a unique positive steady state ϕ^* , and $\lim_{t \rightarrow \infty} \|u(t, \cdot, \phi) - \phi^*\|_\beta = 0$ for every $\phi \in P \setminus \{0\}$. Our numerical simulations in Figure 4 are consistent with this result.

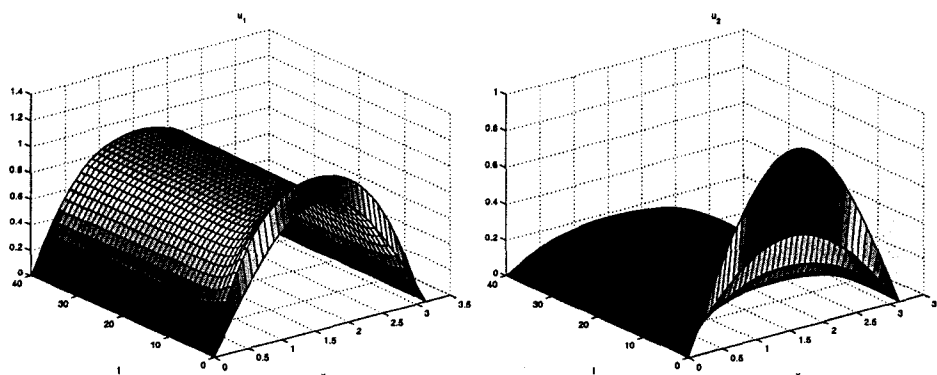


Figure 5.4: Global attractivity of the positive steady state

5.5 Discussion

In this chapter, we consider a reaction-diffusion model with mobile and stationary compartments. We obtain the existence and the computing formula of the spreading speed, and prove that it coincides with the minimal wave speed for monotone traveling waves. This result also shows that the invasion rate of the population can be determined by the linearization of the model system at the trivial solution. We further study the global dynamics of the model in the bounded domain, and give the threshold condition on the global attractivity of either zero or positive steady state. Biologically, this result shows that the population dies out when the zero solution is linearly stable; while the population stabilizes at a unique positive steady state when the zero solution is linearly unstable.

Note that in the case where $Bu = u$ and $\Omega = (0, L)$, we can discuss the critical domain size for the persistence of the population. It has been shown in Theorem 5.3.3

that the stability of the positive equilibrium solution is determined by the sign of λ^* , which is the principal eigenvalue of (5.3.29). In this case, we see from Lemma 5.3.2 that $\bar{\lambda}^* = -\frac{\pi^2 D}{L^2} + f'(0) - \gamma_2$, and

$$\lambda^* = \frac{1}{2} \left[-\frac{\pi^2 D}{L^2} + f'(0) - \gamma_2 - \gamma_1 + \sqrt{\left(-\frac{\pi^2 D}{L^2} + f'(0) - \gamma_2 + \gamma_1 \right)^2 - 4\gamma_1\gamma_2} \right].$$

A straightforward computation shows that if

$$f'(0) - \gamma_2 - \min\{\gamma_1, \gamma_2\} < 0, \quad (5.5.37)$$

then

$$\lambda^* < 0 \text{ for any } L > 0.$$

If

$$f'(0) - \gamma_2 - \min\{\gamma_1, \gamma_2\} > 0, \quad (5.5.38)$$

then

$$\begin{aligned} \lambda^* &> 0 \text{ provided } L > L^* := \pi \sqrt{\frac{D}{f'(0) - \gamma_2 - \min\{\gamma_1, \gamma_2\}}}; \\ \lambda^* &< 0 \text{ provided } L < L^*. \end{aligned}$$

Our results suggest that if the population growth rate at a low density, $f'(0)$, is less than $\gamma_2 + \min\{\gamma_1, \gamma_2\}$, then the population will always die out, no matter what the domain size is. Otherwise, there exists a critical domain size L^* such that the population stabilizes at a positive steady state when the domain size is larger than L^* ; and the population goes extinct when the domain size is smaller than L^* .

We also notice that model (5.1.3) reduces to the classical Fisher's equation if $\gamma_1 = \gamma_2 = 0$ and $f(u) = u(1 - u)$. In this case, (5.2.17) implies that $\Phi(\mu) = D\mu + \frac{1}{\mu}, \mu > 0$, and hence $c^* = \inf_{\mu > 0} \Phi(\mu) = 2\sqrt{D}$. For Fisher's equation with boundary condition $Bu = u$ and $\Omega = (0, L)$, it follows from our discussion that the critical domain size $L^* = \pi\sqrt{D}$.

Chapter 6

Summary

In this chapter, we summarize the results we have obtained in the thesis, and also point out some problems for future research.

Chapter 2 is focused on the global dynamics of a non-autonomous predator-prey model. Extending the earlier work by Song and Chen [45], we consider a more general model and obtain sufficient conditions for the coexistence of the predator and prey species, and for the extinction of the predator species. Our results show that if the zero solution is linearly unstable, which implies that the predator can invade prey successfully locally, then predator and prey species can coexist; otherwise the predator species will die out. Since our conditions are in terms of average integrals of certain functions, they are more natural (and actually weaker) than those given in [45], which are in terms of the maximum and minimum values of the periodic coefficient functions.

In Chapter 3, we study an SIS epidemic model in a patchy environment with periodic coefficients. This model is an extension of the autonomous epidemic model proposed and studied by Wang and Zhao [51]. We give the threshold conditions between the extinction and the uniform persistence of the disease. When the dispersal rates for the susceptible and infectious individuals are the same or very close to each

other, our results suggest that the disease die out eventually if the disease free periodic solution $(S^*(t), 0)$ is linearly stable; and that the population densities of susceptible and infectious individuals stabilize at a positive periodic solution if $(S^*(t), 0)$ is linearly unstable. Moreover, when the dispersal rates for the susceptible and infectious individuals are different, the instability of $(S^*(t), 0)$ implies that the disease is uniformly persistent. In the special case when $n = 1$, we can find the explicit conditions for this threshold type dynamics. It is worthy to materialise the threshold conditions for the case $n > 1$.

We answer an open problem raised by Rass and Radcliffe [41] in Chapter 4. As mentioned in their book, there are no exact results for the asymptotic speed of propagation of infection and traveling waves for models such as (4.1.1) in \mathbb{R}^n or \mathbb{Z}^n . Weng and Zhao [56] has recently addressed this problem for a spatially continuous version of model (4.1.1). Our work is about the spreading speed and traveling waves for the lattice system (4.1.1) in the case where the spatial habitat is the integer lattice \mathbb{Z} . We establish the existence of the spreading speed, and show that this spreading speed coincides with the minimal wave speed for monotone traveling waves.

In chapter 5, we consider a reaction-diffusion model with mobile and stationary compartments, which was proposed by Haderer and Lewis [18]. We study the model in both of unbounded and bounded domain cases. In the first case, we obtain the existence and the computing formula of the spreading speed, and prove that it coincides with the minimal wave speed for monotone traveling waves. In the second

case, we establish the threshold type dynamics for the model, in terms of the principal eigenvalue associated with its linearization at zero. Our results suggest that the population die out when the zero solution is linearly stable; while the population stabilizes at a unique positive steady state when the zero solution is linearly unstable. We even obtain the critical domain size for the population to survive. In addition, we notice that when $\gamma_1 = \gamma_2 = 0$, our model reduces to Fisher's equation. We discuss how the dynamics of the model is similar to that of Fisher's equation. Although model (5.1.3) gives us valuable insights into the spatial dynamics of the population, it is more realistic to assume that the parameters and the reaction function in this model are time dependent in view of the fluctuating environment. As a first step, it is worthy to consider the periodic version of model (5.1.3). We leave it as future work.

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